

Pattern and Process of Fig (*Ficus carica*) Invasion in a California Riparian Forest

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The common edible fig is a subcanopy tree that has invaded many of the remnant riparian forests of California's Central Valley. Fig is unusual in its ability to invade low-light, low-disturbance, native-plant-dominated environments. Dendrochronology combined with regression and spatial analyses allowed us to empirically quantify the expansion rate and spatial pattern of the fig invasion into the native plant community at Caswell Memorial State Park (Ripon, CA) over a 70-year invasion period. Fig uses a combination of short-distance dispersal, which results in constant, linear expansion at source population sites and long-distance dispersal, which eventually leads to high recruitment of satellite populations in ideal environments. Although fig initially experienced a long lag in its invasion rate, at the time of this study, it was expanding at an exponential rate at the landscape scale in Caswell. We identified a number of characteristics intrinsic to the fig population (shade suppression, pollinator presence, highly specialized reproduction, and propagule pressure) as well as extrinsic characteristics of the receiving environment (hydrologic alteration from the construction of a dam, safe sites for juvenile recruitment, and target effects from environmental heterogeneity) that may have influenced the rate and pattern of fig invasion. The Central Valley riparian forests have been reduced to less than 6% of their original area, and invasive fig is a significant threat to the remaining fragments of this important vegetation community. We include suggestions for fig eradication based on knowledge gained in this study.

Nomenclature: Fig, *Ficus carica* L.

Key words: Shade suppression, propagule pressure, target effect, restoration, Central Valley.

Invasion of nonnative plants and animals into wildland areas is regarded as a significant part of global environmental change (Vitousek et al. 1997). Invasive plants and animals have contributed toward many environmental problems, including reductions in biodiversity, endangerment of rare and threatened species, loss of fisheries and forestry resources, and transformation of ecosystem processes, such as fire frequency and nitrogen fixation rates (Mack et al. 2000). Quantifying expansion rates and spatial distributions of aggressive, nonnative species and understanding the processes that control these phenomena are important, not only for understanding basic ecological processes of biological invasions but also to assist restoration programs in identifying troublesome invaders and susceptible native communities.

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Organisms expand into new environments in two ways: (1) outward expansion in an advancing wave-front pattern caused by short-distance dispersal from a source point, and (2) a saltation or punctuated distribution pattern caused by disjunct invasion points developing at multiple sites far away from the source populations because of long-distance dispersal (Henderson et al. 2006; Radosevich et al. 2003; Sakai et al. 2001). Both modes of expansion are important; the first allows an organism to dominate a site at which it has already arrived, whereas the second allows for the colonization of new sites. The invasion rate and spatial pattern of species expanding into new territory are controlled by factors intrinsic to the invading population, often related to propagule supply and dispersal, and by extrinsic factors related to the receiving environment (D'Antonio et al. 2001; Henderson et al. 2006; Kowarik 1995; Rejmánek et al. 2005).

Most invasive species initially spread quite slowly when first introduced into a new area (Mack 1985; Radosevich et al. 2003; Sakai et al. 2001). Many explanations suggested for this initial lag are based on characteristics related to a population's intrinsic ability to produce and disperse large numbers of propagules, including evolutionary adaptation of the invader (Mack et al. 2000), limited initial genetic

Management Implications

Although fig (*Ficus carica*) initially exhibited a substantial lag in its invasion of Caswell Memorial State Park (Ripon, CA), our study found that it was expanding at an exponential rate 70-yr later. Figs' expansion rate and spatial distribution are influenced both by intrinsic factors (shade suppression, pollinator presence, and highly specialized reproduction), as well as by extrinsic factors (hydrology changes and environmental heterogeneity). Because figs are able to invade the remnant riparian forests of the Central Valley, CA, and form dense groves that exclude native vegetation, they constitute a significant threat to this unique and imperiled habitat. Given fig's ability to expand rapidly once critical, intrinsic and extrinsic conditions are met, it would be prudent for managers of riparian areas to eradicate even small populations of fig.

Based on patterns of invasion at Caswell, floodplain positions that are moist well into spring, such as seasonal sloughs or low-elevation alluvial floodplains, are at greater risk of high levels of fig recruitment. However, as demonstrated in Caswell, even higher-elevation riparian sites are not exempt from fig invasion.

Some research has indicated that when controlling invasive plants, satellite populations should be targeted first because reproduction at the edge of an invader's range substantially increases its rate of expansion. In cases where fig is invading shady riparian forests, however, it may be better to first control reproductive source populations, because figs appear to have an extended nonreproductive juvenile period in these habitats.

Figs' extended juvenile period also means that once all adult and juvenile individuals have been eradicated, follow-up control measures at 5-year intervals should be sufficient to catch figs germinating from the soil seedbank before they become reproductive. Thankfully, our monitoring of former fig-invaded sites at Caswell indicates that fig recruitment from the seedbank may be quite limited, an observation that has also been noted for other *Ficus* species.

variation (Lee 2002), limited numbers of pollinators or other mutualists necessary for seed production and dispersal (Randall and Hoshovsjky 2000), and Allee effects resulting from low numbers of reproductive adults (Drake and Lodge 2006; Leung et al. 2004; Taylor and Hastings 2005). Invasive trees have exhibited extended lags between the initial introduction and subsequent range expansion, probably related to their longer generation times (Kowarik 1995).

In addition to factors intrinsic to the invading population, a number of factors related to the landscape being invaded may be important in controlling the expansion and distribution of invasive species. In general, the availability of open sites (i.e., colonization resources) and the context of those sites are key determinants of invasion potential (Foxcroft et al. 2012; Pickett et al. 1987). The available number of "safe sites" for germination (Kowarik 1995); the presence of harsh receiving environments in terms of soil chemistry, climate, or water stress (Harrison 1999; Lonsdale 1999; Randall et al. 1998); the frequency of anthropogenic or natural disturbance (Rouget et al. 2004); and the location of landscape

structures that serve as either barriers or conduits to invasion (Collingham et al. 2000; Radford et al. 2002; With 2002;) have all been identified as important factors in invasion processes. Heavily forested systems in particular often experience significant lag phases early in the invasion process (Essl et al. 2012; Martin et al. 2009).

Empirically derived regression models can quantify the expansion rates of invading organisms. The shape and slope of the growth curve formed by regressing various forms of the cumulative area invaded (arithmetic, log, natural log, square root, or radial range) on time establishes the rate at which nonnative plants expand into unoccupied territory (Barney 2006; Buell et al. 1995; Deckers et al. 2005; Higgins et al. 2001; Lonsdale 1993; Perrins et al. 1993; Pyšek 1991; Pyšek and Prach 1993, 1995; Wangen and Webster 2006; Weber 1998). Not only do these regression models facilitate theoretical model development (Higgins and Richardson 1996; With 2002) but also provide species-specific information that allows for comparative evaluation of invaders (Higgins et al. 2001).

Several techniques, including quadrat frequency counts and mean distance to nearest neighbor, are commonly used to describe and quantify the spatial pattern of organisms distributed on a landscape (Dale 1999; Lo and Yeung 2002; Ludwig and Reynolds 1988; Wong and Lee 2005). A qualitative measure of spatial pattern can also be obtained by comparing the rates of range expansion (number of hectares occupied by at least one invader) vs. the rate of population expansion (total number of individuals) (Wangen and Webster 2006).

The common edible fig (*Ficus carica* L.) has escaped cultivation and has established reproducing populations in many natural areas throughout the world (Hosking et al. 2011). In California, fig has mainly invaded the remnant riparian forests of the Central Valley and nearby foothills, but it is also found along the state's southern coast and on the Channel Islands (Randall 2000). The California Invasive Plant Council ranks fig as a moderate threat overall with severe invasiveness potential and moderate distribution and impact levels (Cal-IPC 2006). Figs are able to invade light-limited forests and form dense stands that crowd out native trees and shrubs (Randall 2000). Fig is a particularly problematic invader in Central Valley riparian forests because these forests have been reduced to less than 6% of their original area because of agriculture and flood control activities (Bay Institute 1998; Geographical Informational Center 2003; Katibah 1984; Vaghti and Greco 2007).

Even though fig is actively invading what has been called "endangered habitat" (Gaines 1980), very little is known about fig as an invader (Randall 2000). The objectives of this study were to (1) quantify the expansion rate and spatial pattern of fig invasion into the native plant community, (2) measure several previously unknown

demographic parameters of wild fig populations, and (3) relate figs' rate and pattern of invasion to intrinsic and extrinsic influences. This information will help land managers identify habitat types susceptible to fig invasion, assess the risk posed by already-existing fig invasions, and develop effective fig eradication programs.

Materials and Methods

Species Description. *Ficus carica* trees grow to a height of about 10 m (30 ft) and have multiple trunks, large deciduous leaves, and latex sap. Figs are unisexual gynodioecious plants (Beck and Lord 1988a) with two sexual forms consisting of female trees ("edible figs") and hermaphroditic trees ("caprifigs"). The fig "fruit" is actually a collective fruit called a *syconium*. Some fig cultivar types can set fruit without being pollinated, but pollination is required to produce viable seeds (Eisen 1901; Kislev et al. 2006; Story 1975, 1976). Figs are pollinated by only one species of wasp, *Blastophaga psenes*, which is very small and lives for up to 2 d once it emerges from syconia on its natal tree (Kjellberg et al. 1988). Receptive fig trees emit unique combinations of volatile compounds (Gibernau et al. 1997; Grison-Pigé et al. 2002), and fig wasps are capable of sensing these chemostimulants and using them to locate fig trees without visual clues (Hossaert-McKey et al. 1994).

Figs trees are one of the earliest known domesticated crops, with evidence of cultivation starting 11,200 yr ago in the Jordan Valley (Kislev et al. 2006). Originally native to southern Arabia, fig's importance as a food source led to its widespread establishment in many countries around the Mediterranean Sea by 500 A.D. (Ferguson et al. 1990). Although figs were brought to California as early as 1769, the fig wasp was not introduced until 1899 when the California commercial fig industry began planting 'Calimyrna' cultivars, which require pollination to set fruit (Ferguson et al. 1990). Fig crop production peaked in the 1930s with more than 16,000 ha (39,536 ac) in cultivation, but commercial cultivation has steadily declined, with only 4,800 ha remaining in 2005 (California Fig Advisory Board 2006). Most commercial fig production has occurred in the middle latitudes (36°N to 38°N) of the Central Valley.

Site Description. Caswell Memorial State Park (Ripon, CA; 37°41'29"N, 121°11'8"W, elevation 12 m; hereafter, "Caswell") is a 105-ha site located on the northern bank of the Stanislaus River, just upstream from its confluence with the San Joaquin River in California's Central Valley. Caswell, like much of California, has a Mediterranean climate, with most rainfall occurring during winter and early spring, followed by hot, dry summer and fall seasons. The construction of the New Melones Dam in 1978 on the

Stanislaus River, approximately 80 km (50 mi) upstream from Caswell, has altered seasonal variation in the channel base flows, with dramatically increased flow volumes during the summer months (July to September) compared with base flows before the dam (CDEC 2012).

The terrestrial areas of Caswell have only been minimally altered by grazing and tree-felling in the past, and its dense, shady forests represent some of the finest remnant stands of riparian habitat in California (Jensen 2003). Caswell contains several vegetation communities (or floristic associations) ranging from the "Great Valley Cottonwood Riparian Forest" along river banks to the "Great Valley Mixed Riparian Forest" in more stable terrain and the "Great Valley Oak Riparian Forest" in the driest and least-disturbed areas of the park (Quinn and Hrusa 1993 after Holland 1986). Caswell's interior contains many sloughs and oxbow lakes that were formed by channel cutoff processes (Michalková et al. 2011) and are seasonally flooded. The vegetation near those sloughs and along the river is quite dense but gradually becomes more open in inland areas, which can be up to 4 m higher in elevation than the river or sloughs are.

Fig has invaded both the cottonwood and mixed-riparian floristic associations at Caswell but is absent from the driest, most-upland portions of the park in the valley-oak floristic association. Although some other Central Valley riparian preserves contain acres of nearly monoculture fig forest (K. A. Holmes, personal observation), Caswell's fig invasion still consists of discrete patches, making it ideal for a demographic study of an invasion in process.

Data Collection. Caswell Memorial State Park was surveyed for fig in 2001 and 2005. A single-invasion site or satellite population was defined as (1) occurring at a distance greater than 20 m from the nearest reproductive individual (a distance presumably evident of intermediate- or long- distance dispersal), and (2) being surrounded by native vegetation. Saplings within a few meters of reproductive trees were presumed to be the result of short-distance dispersal (falling fruit and root suckers) and were, therefore, not counted as new satellite populations. A total of 167 discrete satellite populations were found in Caswell, ranging in size from individual saplings to large groves containing hundreds of mature trees. At each invasion site, the spatial location, diameter of the largest tree, and reproductive status were recorded, and the total number of trees was counted or estimated. Floodplain position (sensu Greco et al. 2008) was also noted: Sites located along the banks of the Stanislaus River were designated *river*, sites located in or beside seasonal sloughs were designated *slough*, and sites located at higher positions on the floodplain than either of the first two categories were designated *terrace*. River and slough sites predominately

occurred within the cottonwood floristic association, whereas terrace sites usually occurred in the mixed riparian floristic association.

As part of the park's management program, fig invasion sites larger than 25 m² (269.1 ft²) were killed with basal bark applications of herbicide in 2002, with follow-up spraying of sapling sites in 2005. Invasion sites were revisited in 2005 and 2006, and the area of each invasion site was estimated by taking two diameter measurements perpendicular to each other and calculating the elliptical area. *Site area* was defined as continuous cover of fig trees without intervening native vegetation. Trunk cross-sections were cut from the largest trees at each invasion site. Fig trees produce distinct growth rings, and those were confirmed to be annual in nature by tissue examination (H. Grissino-Mayer, personal communication) as well as by counting rings on a fig tree of known age (KA Holmes, unpublished data). Ring analysis of the oldest tree at each invasion site was used to establish the age of the site.

Sixty-four sapling-sized satellite populations, most with stem diameters of less than 5 cm (1.97 in), could not be located again in the follow-up surveys; therefore, trunk cross-sections could not be taken. A linear regression between stem diameter and age from 58 satellite populations with similar stem diameters found that stem diameter was a reasonably good predictor for age ($age[yr] = 3.3 + 0.74\{diam[cm]\}$; $F_{1,56} = 258$, $P < 0.0001$, $R^2 = 0.82$) This regression analysis was used to estimate the ages of the 64 satellite populations that could not be age-dated with cross sections.

Rate of Invasion. A chronosequence was created by regressing each satellite population's age on its area, establishing the mean rate at which fig invasion sites expand laterally outward into the native plant community via short-distance dispersal (root sprouts and fallen fruit). Only sites older than 10 yr were included in that regression because we found that fig groves do not expand laterally for their first 10 to 15 yr. Additionally, only sites from which cross sections were taken and age was known by counting annual rings were included in the regression. One site that was constrained on three sides by river and access roads was excluded from the regression. The cumulative number of satellite populations was regressed on time at 5-yr intervals to establish the recruitment rate in Caswell.

By combining the results from the lateral expansion regression model with the known dates of satellite population establishment, a historical reconstruction of the fig population growth curve was created for cumulative area covered by the fig tree canopy. Cumulative canopy cover was regressed by time at 10-yr intervals. Likewise, the range occupied by at least one fig satellite population per hectare was regressed by time at 10-yr intervals. The aerial growth rates of both cumulative canopy cover and

cumulative range occupied were calculated by reporting the slopes of the linear regressions of (1) the natural log of the cumulative area invaded by time, and (2) the natural log of the cumulative hectares occupied by time.

Pattern of Invasion. The spatial and temporal locations of all fig satellite populations were plotted, and their spatial distribution pattern was analyzed at 10-yr intervals with both the variance-to-mean ratios of quadrat frequency counts and the mean distances to nearest neighbor.

The number of satellite populations recruiting in different floodplain positions (river, slough, terrace) was regressed on time at 5-yr intervals and compared; χ^2 analysis was used to evaluate whether certain floodplain positions were preferentially invaded by figs early vs. late in the invasion period.

Fig Demographics. Stem-growth rate was calculated for the largest tree at each invasion site by dividing trunk diameter by tree age. Grove-area growth rate was calculated for each grove by dividing the grove area by the age of the oldest tree found in the grove. Growth rates of tree stem diameter and grove area were compared in different floodplain positions (river, slough, terrace) with ANOVA. Only trees and groves older than 10 yr were included because saplings had significantly slower growth rates.

Two parameters were used to ascertain the likely age of reproductive maturity of fig trees within Caswell: the presence of syconia at individual invasion sites, and the age structure within individual groves.

Ten fig syconia were collected in August 2005 from wild fig populations along each of four different watersheds in central and northern California: Stanislaus River, Merced River, Tuolumne River, and Putah Creek (a tributary of the lower Sacramento River). Seeds were extracted from the syconia and kept refrigerated at 4 C. In June 2006, 400 seeds were randomly selected from each set and were sown in potting soil in plug trays. The trays were placed on a heated mist bench and monitored for 7 wk. Germination levels were recorded at 4 wk and again at 7 wk. To ascertain the viability of the seed bank, fig groves killed at Caswell Memorial State Park in 2002 were monitored for the next 4 yr for germinating fig seeds.

River-Flow Analysis. A base-flow analysis of the Stanislaus River from 1957 to 2012 was conducted for the summer dry-season months (July, August, and September) from the longest continuously operated gauge station (Stanislaus R-Goodwin [SNS]) on the river located near the town of Knights Ferry, CA. The data were obtained from the California Department of Water Resources California Data Exchange Center (CDEC). The data set was divided into two periods: before the dam (1952 to 1978; $n = 66$ mo) and after the dam (1979 to 2012; $n = 101$ mo). The average (mean) flow volume was calculated for each period.

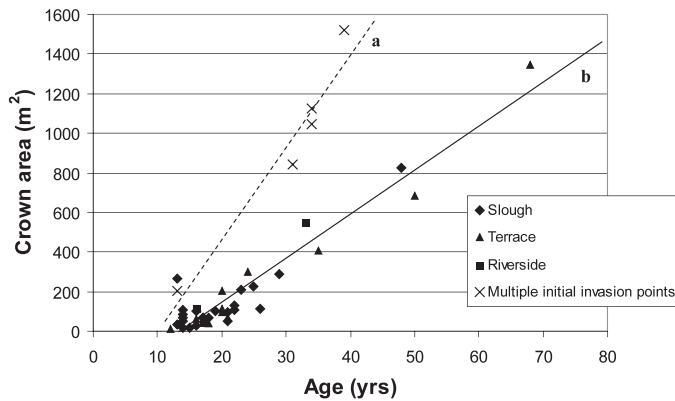


Figure 1. Lateral expansion of fig satellite populations as estimated by regressing satellite population age on crown area (m^2). Satellite populations expanding laterally (a) from multiple invasion points ($\text{area of multiple invasion point groves}[\text{m}^2] = -465 + 47[\text{yr}]$; $F_{1,3} = 47$, $P < 0.006$, $R^2_{adj} = 0.92$), and (b) from single invasion points ($\text{area of single invasion point groves}[\text{m}^2] = -294 + 22[\text{yr}]$; $F_{1,35} = 326$, $P < 0.0001$, $R^2 = 0.90$). Only sites greater than 10 yr old are included.

Statistical Analysis. All regression, ANOVA, and χ^2 statistical analyses were conducted with JMP Statistical Discovery Software (Version 4, SAS Institute, Cary, NC). Test diagnostics were conducted for all tests, including normality of distribution, homogeneity of variance for regression, ANOVA, and the expected cell frequency for χ^2 analysis. The spatial locations of fig satellite populations were mapped in ArcGIS (Version 9.2, Environmental Systems Research Institute [ESRI], Redlands, CA). Spatial analysis on variance-to-mean ratio was conducted in ArcView geographic information system (GIS) (Version 3.3, ESRI) using statistical analysis of geographic information (Wong and Lee 2005). Spatial analysis of mean distance to nearest neighbor spatial analysis was conducted in ArcGIS (Version 9.2, ESRI).

Results and Discussion

Rate of Invasion. The lateral expansion of individual invasion sites and the rate of satellite population establishment both contributed to fig's rate of invasion at Caswell.

Lateral Expansion. At five of the invasion sites, the ages of several of the oldest trees within a single site were less than 4 yr apart. It was, therefore, assumed that those sites were the result of several closely spaced, satellite populations coalescing into a single grove because fig trees in orchard settings are not known to flower before 4 to 7 yr old (Storey 1985). Those five satellite populations had more rapid rates of lateral expansion than did those that were expanding outward from a single, initial invasion point,

and separating them from the rest of the data improved the model fit of both data sets. Each set of data was best fit by linear regression models (single-invasion-point sites: $\text{area}[\text{m}^2] = -294 + 22[\text{age}]$, $F_{1,35} = 326$, $P < 0.0001$, $R^2 = 0.90$; multiple-invasion-point sites: $\text{area}[\text{m}^2] = -465 + 47[\text{age}]$, $F_{1,3} = 47$, $P < 0.006$, $R^2_{adj} = 0.92$; Figure 1).

Satellite Population Establishment. Although the first fig tree invaded Caswell in 1934, there was an 18-yr lag before another fig satellite population was established. Thereafter, the annual rate of satellite population establishment steadily increased, with a sharp increase starting in the 1980s. Herbicide control measures starting in 2002 caused a reduction in the establishment of new invasions sites. The cumulative increase in satellite population establishment was best fit by an exponential regression model (1935 to 2005: $\log[\text{cumulative no. of sat populations}] = -0.3 + 0.035[\text{yr}]$; $F_{1,13} = 570$, $P < 0.0001$, $R^2_{adj} = 0.98$; Figure 2, line a).

Population Growth. The fig population growth curve for cumulative area covered by the fig tree canopy was best fit by an exponential regression model (1935 to 2005: $\log[\text{cumulative area}[\text{m}^2]] = 0.44 + 0.06[\text{yr since invasion}]$; $F_{1,6} = 64$, $P < 0.0002$, $R^2_{adj} = 0.90$; Figure 3a). By 2002, approximately $12,920 \text{ m}^2$ or 1.2% of the total area of Caswell was directly under the canopy of fig trees. The regression model projected that the area would have increased to $16,000 \text{ m}^2$ by 2005 if an eradication program had not commenced. The aerial growth rate of the fig canopy cover (a unitless measure of the rate of spread provided by the slope of the linear regression of the natural log of the cumulative area invaded on time), was calculated to be 0.13.

The total range occupied by at least one fig satellite population per hectare has increased exponentially over time (1935 to 2005: $\log[\text{cumulative ha hosting fig}] = -0.09 + 0.026[\text{yr since invasion}]$; $F_{1,6} = 230$, $P < 0.0001$, $R^2_{adj} = 0.97$; Figure 3b). By 2005, 38% of the total hectares within Caswell hosted at least one fig satellite population. The aerial growth rate of the range occupied by at least one fig satellite population per hectare was calculated to be 0.06.

Pattern of Invasion. During the first 5 decades of the invasion period (1935 to 1985), satellite populations were fairly scattered and the establishment of each new satellite population generally increased the figs' range (the total number of hectares occupied by at least one fig satellite population) (Figure 4a–f). During the most-recent 2 decades (1986 to 2005), satellite population recruitment increased greatly, but a large proportion of the new recruitment occurred as infill between reproductively mature fig groves (Figure 4, g–h) which resulted in an increasingly clustered pattern of distribution, as indicated by both the increasing variance-to-mean ratio values for the

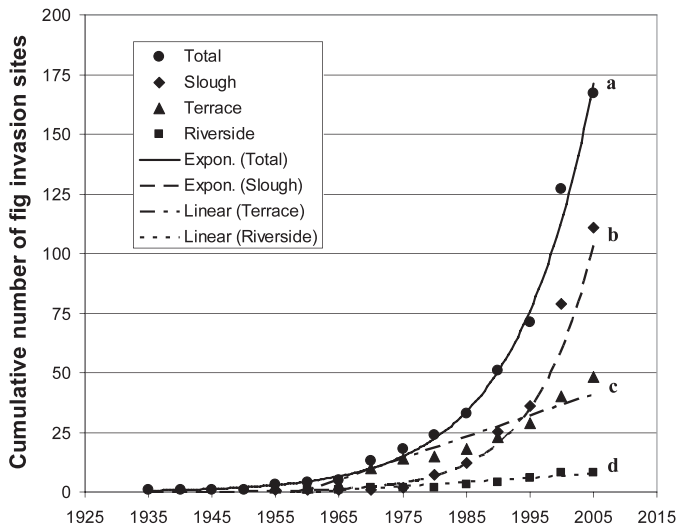


Figure 2. Rate of satellite population establishment as estimated by regressing cumulative number of fig satellite populations on time: (a) all satellite populations in park, 1935 to 2005: $\log(\text{no. of satellite populations}) = -0.3 + 0.035(\text{yr})$, $F_{1,13} = 570$, $P < 0.0001$, $R^2_{adj} = 0.98$; (b) satellite populations along sloughs, 1955 to 2005: $\log(\text{no. of satellite populations}) = -1.4 + 0.047(\text{yr since invasion})$, $F_{1,9} = 142$, $P < 0.0001$, $R^2_{adj} = 0.93$; (c) satellite populations in terrace areas, 1955 to 2005: $(\text{no. of satellite populations}) = -22 + 0.89[\text{yr since invasion}]$, $F_{1,9} = 116$, $P < 0.0001$, $R^2_{adj} = 0.92$; and (d) satellite populations along river, 1955 to 2005: $\text{No. of satellite populations} = -4.0 + 0.16(\text{yr since invasion})$, $F_{1,9} = 78$, $P < 0.0001$, $R^2_{adj} = 0.88$.

quadrat frequency counts (values > 1 indicate a clustering pattern) and the diminishing mean distance to nearest neighbor (Table 1).

Because range expansion preceded the growth of cumulative canopy cover until recently, the surge in population recruitment is occurring as infill, rather than as new range expansion (Figures 3a and 3b).

This process of infilling has occurred mainly along seasonal sloughs, causing a change in the relative recruitment of fig satellite populations within the various floodplain positions (river, slough, terrace) over time. Starting in 1955, satellite population recruitment in terrace areas remained relatively constant (1955 to 2005: $[\text{cumulative no. of terrace satellite populations}] = -22 + 0.89[\text{yr since invasion}]$; $F_{1,9} = 116$, $P < 0.0001$, $R^2_{adj} = 0.92$; Figure 2, line c). In contrast, satellite-population recruitment along sloughs was low early in the invasion process and was followed by a sharp increase starting in the 1980s, resulting in an overall exponential recruitment curve (1955 to 2005: $\log[\text{cumulative no. of slough satellite populations}] = -1.4 + .047[\text{yr since invasion}]$; $F_{1,9} = 142$, $P < 0.0001$, $R^2_{adj} = 0.93$; Figure 2, line b).

Of the 30 fig sites that occurred during the first 50 yr of the invasion (1935 to 1984), 7% ($n = 2$) were found along

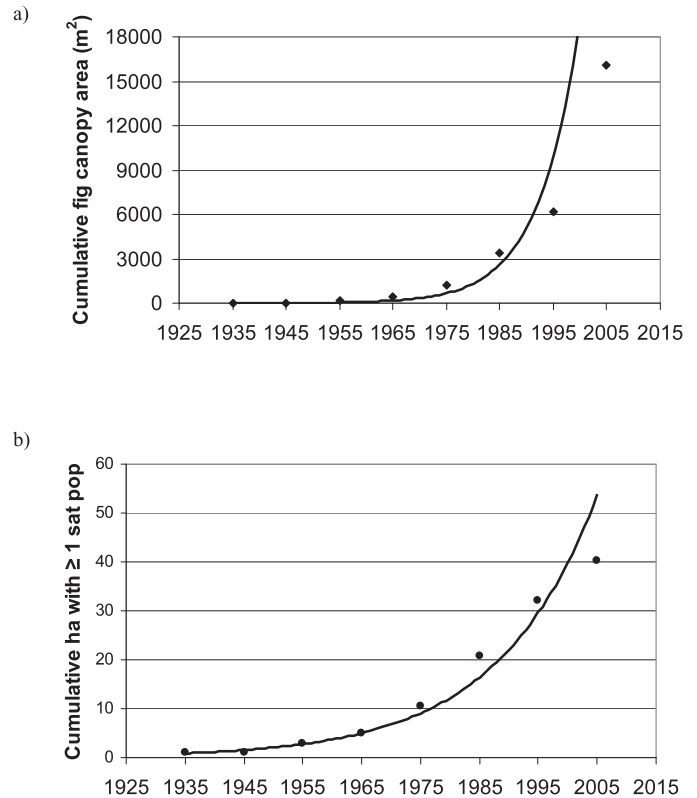


Figure 3. Fig population growth during 70-yr invasion period as estimated by (a) regressing cumulative area covered by fig tree canopy on time, 1935 to 2005: $\log(\text{cumulative area}[\text{m}^2]) = 0.44 + 0.06[\text{yr since invasion}]$, $F_{1,6} = 64$, $P < 0.0002$, $R^2_{adj} = 0.90$; and (b) regressing cumulative hectares occupied by at least one fig satellite population per hectare on time, 1935 to 2005, $\log(\text{cumulative ha}) = -0.09 + 0.026(\text{yr})$, $F_{1,6} = 230$, $P < 0.0001$, $R^2_{adj} = 0.97$.

the river edge, 33% ($n = 10$) were found along sloughs, and 60% ($n = 18$) were found in terrace areas. In contrast, of the 137 fig invasion sites that occurred during the most recent 20 yr of the invasion (1985 to 2005), 4% ($n = 6$) were along the river, 74% ($n = 101$) were along sloughs, and only 22% ($n = 30$) were in terrace areas ($\chi^2 = 18.7$, $P < 0.0001$; Figure 5).

Population Demographics. The growth rates of fig trees were not statistically different among river, slough, or terrace floodplain positions in terms of both rate of stem diameter growth (ANOVA, $F_{2,40} = 0.67$, $P = 0.53$; Table 2) and grove area growth (Kruskal-Wallis $\chi^2 = 0.98$, $P = 0.61$; Table 2).

The youngest tree observed bearing syconia at Caswell was 12 yr old, and that individual was growing in a relatively open, sunlit area. Most of the individuals younger than 15 yr did not appear to be reproductively mature. Age structure within fig groves also provides information about fig tree reproductive maturity; the age of the second-oldest

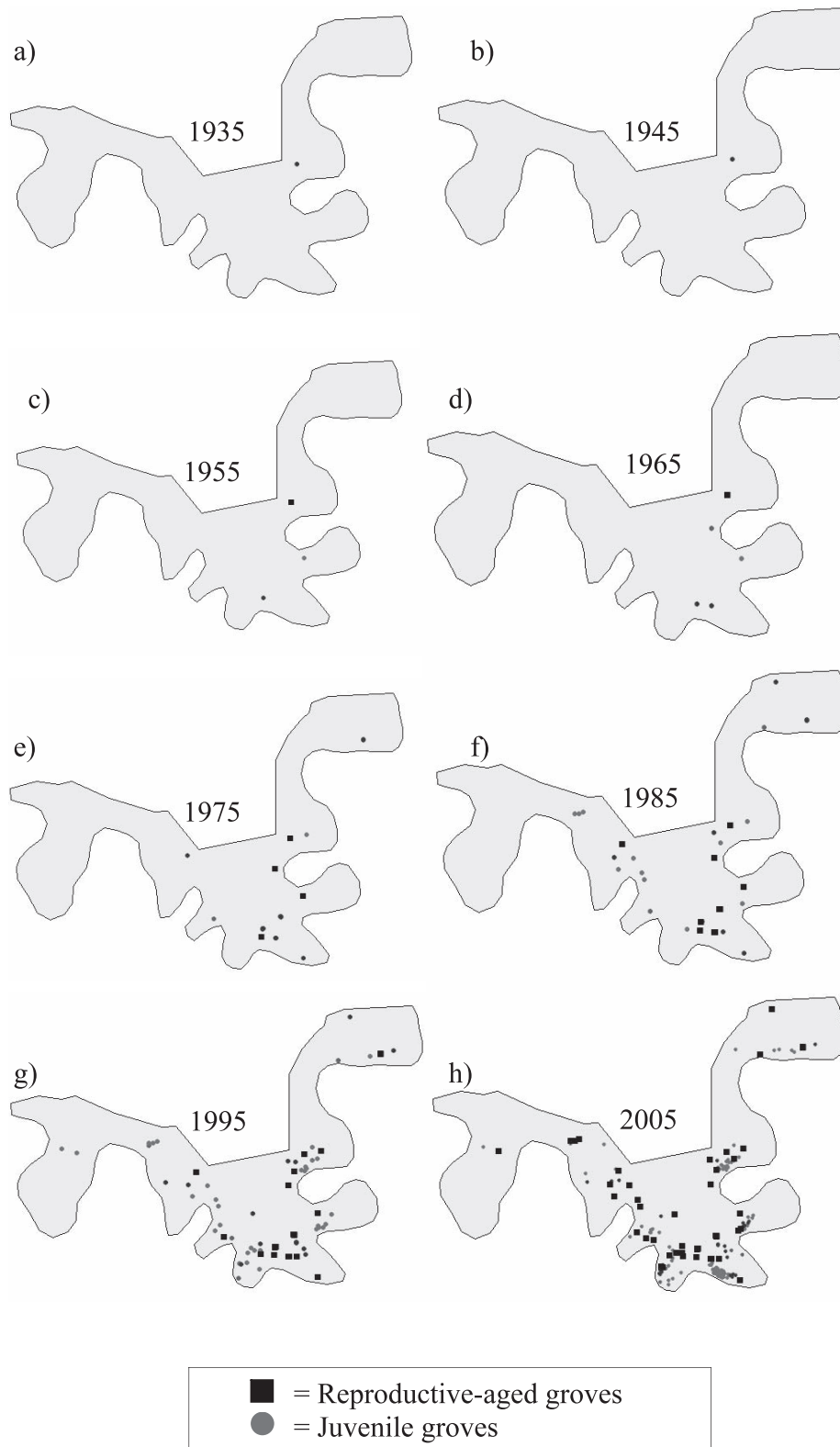


Figure 4. Spatial location of fig satellite populations at 10-yr intervals during 70-yr invasion history at Caswell Memorial State Park.

Table 1. Measurements of spatial pattern of fig satellite populations at 10-yr intervals during the 70-yr invasion period: variance-to-mean ratio of quadrat frequency counts and mean distance to nearest neighbor. Variance-to-mean ratios that were significantly different than 1 at $P < 0.05$ are denoted by asterisks (*) and indicate a clustered distribution pattern.

Year	No. of satellite populations	Variance-to-mean ratio	Mean distance to nearest neighbor
1935	1	—	—
1945	1	—	—
1955	3	1.3	421.6
1965	5	0.3	156.2
1975	18	4.8*	83.9
1985	33	4.3*	62.2*
1995	71	7.1*	42.9*
2005	167	18.7*	22.5*

tree at individual fig invasion sites ranged from 11 to 40 yr younger than the oldest tree, and single, solitary trees up to 21 yr old were found without evidence of either sexual or vegetative understory recruitment.

Seeds extracted from syconia collected from fig populations in four different watersheds were all highly viable, with germination levels ranging from 86 to 93%. Those germination levels are similar to those reported for commercial figs (Lisci and Pacini 1994). The seed bank in the soil underneath fig groves does not appear to be highly viable, however. At two of the larger, former fig sites (an area totaling 2,200 m² and formerly host to hundreds of reproductive trees), only 10 to 20 seedlings were observed

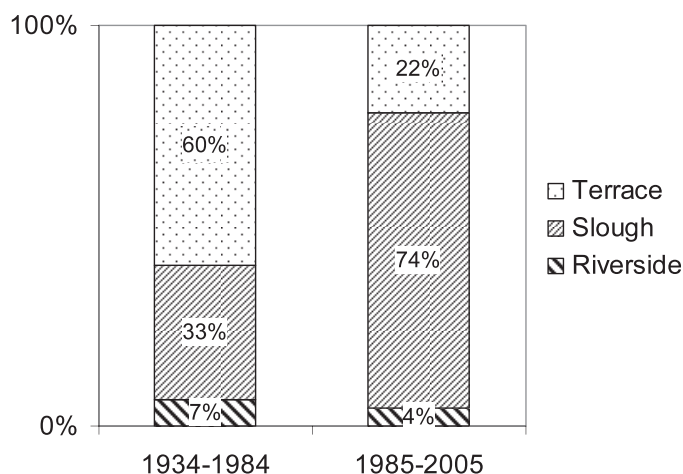


Figure 5. Proportions of fig satellite population recruitment by floodplain position (terrace, seasonal sloughs, riverside) early (1934 to 1984) vs. late (1985 to 2005) in the invasion period; χ^2 analysis found proportions of early vs. late terrace and slough populations to be significantly different ($P < 0.0001$).

Table 2. Fig tree growth rates in different habitat types in terms of (a) trunk diameter (cm yr⁻¹) of oldest tree in each grove, and (b) grove area (m² yr⁻¹). Only sites greater than 10 yr old are included. Only single invasion-point groves included in grove-area analysis. Responses not significantly different at $P < 0.05$.

Floodplain position	Growth rate	
	mean \pm SE	<i>N</i>
a) Stem diam growth rate (cm yr ⁻¹)		
Riverside	0.84 \pm 0.12	4
Slough	0.93 \pm 0.06	23
Terrace	0.99 \pm 0.06	16
b) Grove area growth rate (m ² yr ⁻¹)		
Riverside	8.8 \pm 4.1	3
Slough	6.6 \pm 1.1	20
Terrace	8.7 \pm 1.8	10

sprouting each year from 2004 to 2006. It is possible that herbicide soil residues account for low germination during the first year following herbicide treatment (Holmes and Berry 2009). By 2004, herbicide residues did not appear to be affecting germination, however, because many other species were observed sprouting at former fig sites.

River Flow Analysis. The dry-season analysis of flow records from summer months (July, August, and September) before building the dam (1952 to 1978; $n = 66$ mo) shows the average monthly flow volume before construction of the dam was 3,692,652 m³ mo⁻¹ (2,994 ac-ft mo⁻¹) and after completion of the dam (1979 to 2012; $n = 101$ mo), it was 43,843,917 m³ mo⁻¹ (35,545 ac-ft mo⁻¹), which represents a more than tenfold increase in summer base flow.

Population Growth. Fig has clearly exhibited several dispersal distances during its 70-yr history of invasion in Caswell. We found that fig groves 30 yr and older contained hundreds of reproductive trees and saplings. Presumably, that was because of short-distance dispersal occurring through both root suckering (Randall 2000) and through seeds from fruit falling near reproductive trees (Lisci and Pacini 1994). Invasion theory predicts that short-distance dispersal alone will result in linear expansion rates (Shigesada et al. 1995). Our regression of grove size on grove age indicates that figs do expand laterally outward from reproductive individuals at a constant linear rate, although that rate differs depending on whether the invasion is associated with single or multiple invasion points.

We also found that during the past 2 decades of the invasion period, fig satellite populations were recruiting at distances of 20 to 200 m from reproductively mature fig

groves. A variety of animals are known to consume and effectively disperse fig syconia (Debussche and Isenmann 1989; Lisci and Pacini 1994; Nogales et al. 1999). Fig seeds have been observed in animal scat in Caswell (K. A. Holmes, personal observation), and vertebrate transport probably accounts for satellite population recruitment at intermediate and long distances from mature fig groves in the park.

Theoretical modeling efforts indicate that plants using both short- and long-distance dispersal strategies may be more invasive (Moody and Mack 1988; Simberloff 2009), and case studies have found that many aggressive, invasive species exhibit multiple dispersal distances (Deckers et al. 2005; Gilbert et al. 2004; Kirk et al. 2011; Lonsdale 1993; Perrins et al. 1993; Richardson et al. 2000; Shigesada et al. 1995; Wangen and Webster 2006). In the case of fig, when lateral linear growth resulting from short-distance dispersal was combined with exponential recruitment of satellite populations at intermediate and long dispersal distances, the overall population growth rate was exponential. Fig's aerial growth rates of 0.06 (range occupied by at least one satellite population ha^{-1}) and 0.13 (area under fig canopy cover) are similar to those of many other aggressive, invasive species, which generally have been found to range from 0.026 to 0.13 (Higgins et al. 2001).

Intrinsic Influences on Rate and Pattern. Figs in commercial orchards are reported to reach reproductive maturity in as little as 4 yr (Storey 1985). However, both the lack of evident syconia on most fig trees younger than 15 yr and the age structure observed within groves indicate that figs at Caswell are experiencing delayed reproduction compared with those in commercial orchards. The understory at Caswell, like many riparian forests, is quite shady. Reduced light can suppress plant growth and development (Coa and Ohkubo 1999; Kohyama 1980; Martin et al. 2010) and may explain the observed delay in reproductive maturity in figs at Caswell. Early reproduction is often associated with a propensity for invasiveness (Kolar and Lodge 2001; Kowarik 1995; Rejmánek and Richardson 1996), and an extended juvenile stage due to shade suppression may have increased generation times and contributed to figs' initial expansion lag.

Fig wasps were introduced in California orchards in 1899 (Ferguson et al. 1990), 35 yr before the initial fig invasion at Caswell. The wasps' flying range may be quite limited in latitudes south of 40°N (Valdeyron and Lloyd 1979), however, and one mark–recapture study found that many fig wasps remain within a few meters of their natal tree (Kjellberg et al. 1988). It is likely that early in the fig invasion process at Caswell, populations of fig wasps were not widespread or naturalized in wildland areas of northern California. Even today, California fig growers use the practice of *caprifigation*—hanging bags of wasp-filled caprifig syconia throughout their orchards—to ensure

successful pollination (Ferguson et al. 1990). Additionally, although technically gynodioecious, fig trees are actually functionally dioecious because the hermaphroditic caprifig produces very few viable seeds because of fig wasp ovule parasitism and poor pollen receptivity (Beck and Lord 1988b).

The absence of mutualists (Randall and Hoshovsky 2000) and Allee effects created by limited numbers of reproductive adults (Drake and Lodge 2006) are both thought to restrict invasive organisms early in invasion processes. It is likely that some component of the fig reproductive system was absent in the park early in the invasion process because recruitment was virtually nonexistent within a few hundred meters of reproductively aged fig groves in Caswell during the first 5 decades of the invasion. The recruitment that did occur during that time was probably the result of long-distance dispersal of propagules from reproductive fig trees outside of Caswell, which contributed to the scattered spatial distribution pattern evident before the 1980s.

Fig wasps now appear to be widely naturalized in wildland settings in northern and central California; the high levels of viability we found in seeds collected from wild fig populations along four watersheds in California in 2005 would only have occurred if the syconia were being pollinated by fig wasps (J. Dyole, personal communication). The dramatic increase in satellite-population recruitment near reproductive-aged figs during the past 2 decades of the invasion, which created a clustered spatial pattern, may indicate that fig wasps had become naturalized in Caswell and that local propagule production had, therefore, greatly increased.

Extrinsic Influences on Rate and Pattern. Although seasonal sloughs account for only a small portion of the total area at Caswell, more than two-thirds of the sites invaded during the 70-yr invasion period were found along those sloughs. Seasonal sloughs are inundated with water most winters and are often moist well into summer, which is in contrast to adjacent terrace areas that are inundated only occasionally during flood events (K. A. Holmes, personal observation). Fig seeds require constant moisture for successful germination (Lisci and Pacini 1994), and sloughs may provide safe sites for fig survival in the germination and seedling stages.

An apparent paradox revealed by this study is the shift in the relative rate of recruitment of fig seedlings within floodplain position; early in the invasion process (1934 to 1985) recruitment took place primarily in drier terrace areas, but after 1985, most recruitment occurred in moister, seasonal sloughs. This seeming paradox may be the result of interactions between propagule pressure, dispersal distances, spatial variations in the receiving environment, and changes in the Stanislaus River's base-flow levels.

Invasion biologists have noted that when propagules are introduced into a new range with substantial spatial, environmental stochasticity, many often land in unsuitable sites, reducing establishment success (Sax and Brown 2000) and creating time lags in invasion processes. However, increased propagule pressure (D'Antonio et al. 2001) and changes in the receiving environment that make it more habitable to the invader (Simberloff 2009) can greatly accelerate invasion rates, even in spatially heterogeneous environments.

Early in the invasion process at Caswell, fig source populations would have occurred outside the park, and the distances required for successful propagule dispersal would probably have been quite long. Propagule pressure would, therefore, have been light during that period.

Furthermore, because the seasonal sloughs constitute a relatively small target area within the park, it would have been unlikely for propagules to land in those moist environments; instead, most of them probably landed in drier terrace sites. Although a few fig satellite populations did successfully recruit into terrace areas (perhaps during years with exceptionally high levels of spring precipitation), presumably most of the propagules landing in the drier areas of the park did not survive. That would have contributed to the low recruitment rates, the expansion lag, and the scattered spatial pattern evident early in the invasion period.

As the fig groves that did successfully recruit early in the invasion period within the park reached reproductive age, and all of the components of the figs' complex reproductive system became established, propagule pressure would have increased dramatically, and distances required for successful propagule dispersal would have been much shorter. Although seasonal sloughs would still have presented a relatively small target area within the park, high propagule pressure combined with shorter required dispersal distances appeared to have allowed increasing numbers of fig propagules to reach the relatively small, but ecologically ideal, seasonal sloughs that lace the park.

Recruitment rates into sloughs may also have been affected by the damming of the Stanislaus River in 1978. The significantly higher base flows resulting from the dam may provide greater floodplain moisture along the margins of the sloughs and oxbow lakes within Caswell, possibly increasing the length of time that soil moisture conditions are favorable for fig recruitment. These changes in summer base flows, starting in 1978, may have contributed to the surge in fig recruitment observed along sloughs in the park during the 1980s. Flow regulation by dams has been shown to facilitate nonnative species invasions in riparian wetlands in Australia (Catford et al. 2011).

Although figs continued to recruit at low levels into the drier terrace areas later in the invasion period, it is the relatively recent exponential increase in recruitment along

sloughs located within a couple hundred meters of mature fig groves that is driving the exponential increase of satellite populations as well as the increasingly clustered spatial pattern of infilling.

Restoration Implications. Understanding the complex interactions between landscape heterogeneity and propagule pressure is critical to the study of invasion biology and can help inform management efforts (Caughlin et al. 2012). Relevant to the assessment of fig as an invader is that, before the commencement of the eradication program, its recruitment into previously unoccupied areas in Caswell had steadily increased over time with no sign of diminishing. Models and case studies of invasions often find that invading populations reach a saturation phase wherein the growth rate slows because of the lack of niche space and available resources (Arim et al. 2006; Barney 2006; Dietz et al. 1999; Radosevich et al. 2003; Wangen and Webster 2006), but that has not yet happened to the fig populations at Caswell. Furthermore, it is quite likely that without management intervention, fig would have continued to expand exponentially.

A large number of the satellite populations in the park had either not yet, or only recently, reached reproductive maturity. If those populations had been allowed to become fully mature, propagule pressure would have increased substantially. When propagule pressure is high, even less-suitable habitats may become heavily invaded (D'Antonio et al. 2001; Rejmánek et al. 2005; Richardson and Rejmánek 1999). Although we found that sloughs within the cottonwood floristic association were the initial habitat type to experience an exponential rate of satellite population recruitment, higher elevation sites in the mixed riparian and valley oak floristic associations may also have been susceptible to increased rates of invasion if propagule pressure had substantially increased. Because the growth rates of fig trees (in terms of both stem diameter and grove area) were not statistically different among riverside, slough, and terrace-floodplain positions, once established, figs would have been capable of growing well in a wide range of environmental conditions.

Other woody, shade-tolerant nonnatives invading forested systems experience long delays in their expansion (Essl et al. 2012; Frappier et al. 2003; Martin et al. 2009; Wangen and Webster 2006), and that increases the risk that they may not be perceived as invaders by land managers until their population explodes. Fig canopy in Caswell, for example, expanded to cover more area during the last 7 yr of its invasion history than it had during the entire preceding 60 yr. Misidentification of potential invaders can delay the implementation of control programs, making eradication much more time-consuming and costly. Based on the study results at Caswell Memorial State Park, it would be advisable for managers of riparian

areas in Mediterranean environments to eradicate even incipient populations of fig.

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