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UNIVERSITY OF CALIFORNIA

Santa Barbara

Vegetation Establishment Following Floodplain Restoration in Mediterranean-climate
California

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Environmental Science and Management

by

Oliver Soong

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March 2017

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Vegetation Establishment Following Floodplain Restoration in Mediterranean-climate

California

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Oliver Soong

ACKNOWLEDGEMENTS

I would like to thank all of the people without whose aid none of this would have been possible. The Delta Stewardship Council, Delta Science Program (grant no. U-05-SC-058), the National Center for Ecological Synthesis and Analysis, Conservation International, and the Bren School all provided financial support along the way. Chris and Lee Robinson and the Robinson Cattle Company have my deepest thanks for their exceptional hospitality and assistance. To my advisor, Frank Davis, I say thank you for your advice, assistance, guidance, support, and patience through the years. To the other members of my committee, Tom Dunne and Carla D'Antonio, I offer my thanks for your extensive feedback and advice, which has improved this work immensely.

There are many who have helped in innumerable seemingly innocuous and yet utterly essential ways. I thank the Bren School and ERI and especially the staff, starting with Kristine Falloon, for their support and aid over the years. Karen Dulik, Kevin Faulkenberry, and the staff at CADWR, Fresno provided much support and data on the Robinson Reach. Lee Harrison, Tom Dudley, John Melack, and Dave Valentine provided data, equipment, and facilities, for which I am grateful. Thanks you, Patrick, Theresa, Jason, and Maki and everybody else from the biogeog lab, for your friendship and thoughtful discussions on- or off-topic. Thanks as well to my fellows in commiseration, Brian, Blair, Ali, Erin, Ian, Son, Ben, Annie, and all those who have responded to my complaints, questions, and doubts with grace, sympathy, and clarity. Finally, I would like to thank my family and in particular my parents, Norman and Sabrina, without whom I would not be where I am today.

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ABSTRACT

Vegetation Establishment Following Floodplain Restoration in Mediterranean-climate California

by

Oliver Soong

Although herbaceous communities are important components of floodplain ecosystems, the factors constraining their restoration and post-restoration dynamics are poorly understood. Over the decade following restoration of a 3.2-km reach of the Merced River and floodplain in California, we tracked herbaceous community composition to distinguish floodplain habitats and utilized perturbations from revegetation treatments and post-restoration flooding to generate community assembly rule hypotheses regarding treatment effectiveness and persistence, with a particular interest in native perennials capable of suppressing non-natives over time if undisturbed. Revegetation treatments comprised combinations of sowing a sterile cover crop, sowing native species, and inoculating mycorrhizae. Most surveyed floodplain areas comprised a low terrace characterized by exceptionally droughty soils, relatively deep groundwater, and occasional flooding lasting into summer. Few species could tolerate both flood and drought to this extent, and the flood year community was generally distinct from that in non-flood years. Both communities were dominated by ruderals capable of avoiding stress and re-establishing following

disturbance, including many non-native annual grassland species. Only *Artemisia douglasiana* responded to the treatments, as most seeded native species failed to establish, including those native perennial grasses expected to suppress non-native annuals, while other seeded native species either established adequately from natural dispersal or failed to persist through moderate flooding. Neither the cover crop nor mycorrhizal inoculation had any meaningful effect. Restoration efforts in naturally ruderal-dominated habitats may be better spent allowing natural regeneration, addressing particularly noxious invasives, and identifying or constructing habitats supporting long-lived native perennials.

Although originally developed for population sizes and population growth rates, modern capture-recapture models can estimate demographic rates in complex situations: multistate models for multiple study sites and stage-structured populations, superpopulation entry probability models for recruitment, and multievent models when state assessments are uncertain. However, combinations of these complications, such as recruitment studies with uncertain state assessments, are common, yet no single model has explicitly incorporated all of these elements. Ultimately, these models estimate the same fundamental population process with the same general approach, and we combine them in a generalized hidden process model based upon a simple discrete state and transition population model with Poisson recruitment that can estimate how recruitment and survivorship rates vary with respect to measured covariates from uncertain state assessments for a stage-structured population at multiple sites. Although closely related to the motivating models, the generalized model relaxes the Markov assumption. While we provide the distributions necessary to implement Bayesian data augmentation methods, we also provide an efficient analytical likelihood with a compact parameter space that is applicable in the absence of

density-dependent mortality. As a demonstration, we estimate the influence of several covariates on recruitment and survivorship rates from uncertain observations of *Salix gooddingii* seedlings at different locations along a riparian gradient, and we use simulations to examine variation in the precision of estimated parameters.

In Mediterranean climates, cottonwoods and willows often exhibit high germination and seedling mortality rates, with recruitment occurring primarily in the occasional year when favorable spring floods improve survivorship. However, along the Robinson Reach of the Merced River, both germination and mortality rates appeared to be atypically low. To understand why these rates were so low along this recently restored flow-regulated, gravel-bedded stream, we surveyed *Populus fremontii*, *Salix exigua*, and *Salix gooddingii*, estimated germination and survivorship rates, and examined their correlations with factors expected to constrain recruitment, namely seed release, seed arrival, moist germination beds, light levels, groundwater depth, groundwater recession rates, and shear stress. Germination/initial establishment rates were low due in part to low seed arrival rates. Only *Salix gooddingii* was abundant enough to model in detail, and while moist germination surfaces increased germination/initial establishment, rates were low overall. Survivorship rates for *Salix gooddingii* seedlings and for small individuals were not correlated with any examined covariates. Seedlings tolerated moderate competition, and the absence of major scouring, even during 6 year flows, enabled survival at sites with sufficiently shallow groundwater that seedlings were unaffected by groundwater recession rates.

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I. Introduction

Riparian habitats in the American West are a glimmer of what they once were, due to the combined pressures of land clearing and flow regulation. For example, an estimated 98% of riparian forest along the Sacramento River in California has been lost since 1848 (Roberts et al. 1977), while the median annual discharge of the Merced River in California has been reduced to less than 30% compared to the pre-dam period (CADWR 2016). As awareness of the ecological costs has grown, so too have efforts to restore riparian forests and mitigate the degradation of floodplain habitats (Bernhardt et al. 2005). Such activities require an understanding of where species occur, how they get there, and why they remain there. Furthermore, because full natural flows are so rarely restored, it is particularly important to examine these questions under regulated flow conditions.

Cottonwoods and willows are both common riparian forest species and particularly affected by flow regulation. The brief period during which they release their seeds often occurs as snowmelt-derived spring floods recede (Stella et al. 2006). These seeds are dispersed by both wind and water to moist and bare flood deposits, where they germinate within days (Fenner et al. 1984, Braatne et al. 1996). As floodwaters recede, the roots of these seedlings grow deeper, following the receding water table and its moist capillary fringe. Seedlings that germinate too high on the river bank or whose roots grow too slowly are unable to keep their roots moist and are killed by drought, while seedlings that germinate low on the river bank are vulnerable to being scoured by future flood flows (Mahoney & Rood 1998). Nonetheless, cottonwoods and willows do occur along regulated rivers, and to facilitate management efforts, it would be useful to know how recruitment dynamics differ under regulated flow conditions.

Riparian forests may be the predominant riparian habitat, but herbaceous vegetation is more important than the amount of research done on it would suggest. Whereas most riparian plant biomass is contained within trees, most plant species are herbaceous (Gilliam 2007). Whereas trees provide canopy structure, herbs help reduce erosion and stabilize banks (Simon & Collison 2002) and contribute to nutrient cycling and disturbance response (Whigham 2004). Some parts of the floodplain are even dominated by herbs (Conard et al. 1977). No riparian ecosystem is complete without herbaceous vegetation, and yet there is much to be learned about which conditions favor which species and the extent to which management and restoration activities can alter herbaceous communities.

Recruitment and mortality rates are often estimated from survey data, but plants can be more elusive than they are commonly considered. Seedlings, small plants, plants that resprout, and dormant plants can easily be overlooked. Capture-recapture models are commonly used to account for false absences in survey data, and while they have been most commonly used for animal studies (Lebreton et al. 1992), they have also been applied to plants (Shefferson et al. 2001). Although advances in capture-recapture models allow the estimation of recruitment rates (Schwarz & Arnason 1996), spatially variable demographic rates (Arnason 1972), or uncertain condition assessments (Pradel 2005), no model incorporates all three. Such a model would enable a more rigorous estimation of how seedling recruitment rates vary across the river bank when seedlings might be missed and their condition is uncertain.

This dissertation examines the herbaceous and woody plant communities along a recently-restored and flow-regulated reach of the Merced River for the broad purpose of understanding which species occur there and what factors lead to this outcome, in the

process developing a capture-recapture model capable of estimating spatial variations in recruitment rates from uncertain observations. The first chapter follows the development of post-restoration herbaceous vegetation to determine whether distinct communities established, whether such communities aligned with common wetland/upland gradients, and whether restoration treatments could alter their development to favor desirable native species. The second chapter draws upon existing capture-recapture models capable of estimating recruitment, models capable of estimating spatially variable demographic rates, and models capable of estimating demographic rates when the condition of observed individuals is uncertain, and derives a novel model that incorporates all three of these elements. In the third chapter, surveys of seedlings and other small individuals of three cottonwood and willow species are compared against seed release, seed arrival, the availability of moist germination beds, light levels, groundwater depth, groundwater recession rates, and shear stresses during peak flows to determine to what extent and why germination and survivorship rates estimated along this reach of flow-regulated river differ from those reported in the existing literature.

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2. Restoring Floodplain Herbaceous Communities in Mediterranean-climate California

Introduction

Decades of well-intentioned water resources development, often in the form of dams, levees, and straightened channels, have degraded river systems worldwide (Baron et al. 2002), driven in part by damage to riparian vegetation (Sweeney et al. 2004). Plant cover diminishes erosion (Micheli et al. 2004) by slowing flood flows and stabilizing river banks and floodplain soils (Simon & Collison 2002). Floodplains provide unique habitats, which in Mediterranean environments are more productive for more of the year than surrounding upland habitat, and support a greater diversity of plants and animals than surrounding areas (Holstein 1984). Terrestrial vegetation helps support aquatic food webs and fisheries through allochthonous nutrients, shading, and the habitat diversity caused by coarse woody debris (Wallace et al. 1997; Gurnell & Sweet 1998; Kelly et al. 2003; Hafs et al. 2014).

Forests dominate sufficiently stable floodplains, and riparian revegetation has generally been synonymous with planting trees and shrubs (Carothers et al. 1990), but in California and similar such Mediterranean climates, herbaceous vegetation deserves more attention than is typically given. Herbs comprise most of the diversity, both native and non-native (Gilliam 2007), and can provide bank stabilization and erosion control in some settings (Simon & Collison 2002). The herbaceous layer is important in disturbance response, nutrient cycling, phenology, and seedling competition (Whigham 2004). Herbaceous species also can dominate in some areas of the floodplain, such as those adjacent to the channel and frequently disturbed (Conard et al. 1977; Stromberg et al. 2007). In California in particular, riparian forests often have sparse tree canopies with significant herbaceous

communities, under both historical and modern flow regimes (Thompson 1961; Stella et al. 2003).

Restoration has the potential to reverse the degradation of riparian habitats, but riparian restoration targets are especially difficult to define. The full restoration of riparian processes may be most effective (Wohl et al. 2005), but in California, societal demands mean it is impossible to fully restore flow regimes and reference conditions. However, it is unclear whether these riparian processes can be spatially downscaled to support functional yet diminished floodplains suited to the modern flow regime. Revegetation targets are often informed by local and historical reference conditions (Palmer et al. 2005), but such patterns, defined largely by historical flows, may not be more than suggestive of those appropriate to modern conditions. In other words, when riparian processes cannot be fully restored, it becomes especially important to understand how they structure riparian vegetation in order to define appropriate restoration targets.

Ideally, restoration accelerates the natural development of self-sustaining communities (Bradshaw 1987) by alleviating the filters that constrain community assembly (Hobbs & Norton 2004). Riparian vegetation is generally arranged along a wetland/upland gradient extending away from the river channel (Conard et al. 1977; Vaghti & Greco 2007), reflecting correlated differences in floodplain age, flood regime, water table depth, and soil properties such as texture and organic content (Hupp & Osterkamp 1985; Bechtold & Naiman 2006). In other words, the constraining filters and restoration targets vary by landform. However, despite a general understanding of the basic influences on patterns of riparian vegetation, restoration in practice requires a detailed knowledge of which species are constrained by which filters on which landforms. For revegetation activities, particularly

noteworthy groups of species are those capable of establishing unassisted, those limited by seed supply, those requiring a degree of facilitation (e.g., mycorrhizae), and those that otherwise appear biophysically incapable of establishing.

Additionally, significant restoration resources are often devoted to excluding non-native species, and there is a particular interest in constructing resistant native communities. The pre-settlement herbaceous vegetation of Californian riparian systems and their modern invasions have been little studied, but riparian floodplains are generally invasible and often support more non-native species than the surrounding uplands (Hood & Naiman 2000). In California, some of these non-native species, such as *Erodium cicutarium* and *Bromus diandrus*, are also common in the nearby uplands, which consist of better-studied annual grassland. Native perennial grasses, such as *Stipa pulchra* and *Elymus triticoides*, may have historically dominated such mesic portions of the Central Valley and some riparian floodplains (Hamilton 1997; Holstein 2001; D'Antonio et al. 2007). Although modern annual grasslands may be maintained by the competitive dominance of non-native annual species in some areas (Dyer & Rice 1997), established native perennial grasses can sometimes resist invasion by non-native species (Corbin & D'Antonio 2004; Reever Morghan & Rice 2005).

It remains unclear how best to restore Mediterranean-climate riparian herbaceous communities, from the appropriate reference communities to the challenge of modern flow regimes to the technical details of specific revegetation practices. To better understand how fluvial processes and biophysical conditions influence the assembly of herbaceous floodplain communities, we tracked herbaceous vegetation in monitoring plots established after restoration of a 3.2-km reach of the Merced River and adjacent floodplain in

California. We asked whether restored floodplain habitats supported distinct herbaceous communities and whether restoration treatments could alter those patterns by enabling the establishment and persistence of particular species of interest. More specifically, we hypothesized that post-restoration herbaceous communities would demonstrate a toposequence with plant assemblages in wet areas near the river developing towards native freshwater emergent wetlands and drier portions of the floodplain further from the river trending towards mesic grasslands dominated by native perennial grasses. Reflecting stated objectives, we hypothesized that the herbaceous revegetation treatments applied in this case study—seeding native species, seeding a sterile cover crop, and mycorrhizal inoculation—would accelerate the establishment of a diverse and self-sustaining community dominated by native species capable of outcompeting non-natives. More broadly, we hypothesized that seeding would be effective for all seeded native species, without indications of either adequate natural seed supply or biophysical unsuitability to the restored floodplain.

Methods

Study Site and Restoration

This study took place at the Robinson Reach (lat 37°29'30"N, long 120°29'30"W) of the Merced River, near Merced, California. The reach is situated at the margin of California's Central Valley, by the Sierra Nevada foothills. Here, the Merced River is alluvial and gravel-bedded. The Mediterranean climate normal has monthly temperatures ranging from 2–36°C, and 26 cm of precipitation (81% of the annual total) occurring between November and March (NOAA 2002). Two upstream dams, New Exchequer and McSwain, are regulated largely for agriculture and fisheries management, discharging generally uniform

flows interrupted by winter storms, management releases, and extreme snowmelt years (Figure 2.1).

Restoration began in 2001 to mitigate damage to the Chinook salmon (*Oncorhynchus tshawytscha*) fishery resulting from historic gravel mining and catastrophic flooding in 1997 (CADWR 2002). Beyond re-engineering the channel to accommodate the prevailing regulated flow regime, old gravel pits were first filled with extremely gravelly coarse sand excavated from nearby deposits and then leveled. The new floodplain was a broad, flat terrace situated at the designed bankfull elevation, roughly 1.2 m above the baseflow water surface. The floodplain contained several artificial features, such as a backwater slough, but treatments and surveys were restricted to flat areas (CADWR & CADFG 2003).

Revegetation began in 2002 (Figure 2.1). We focus here on the three broadcast herbaceous treatments (CADWR & CADFG 2003), a sterile barley cover crop (BAR), seeding native species (SEED), and mycorrhizal inoculation (MYCO). Besides untreated controls, these treatments were applied in four combinations (B, BS, BSM, and SM, where the component treatments are further abbreviated; Table 2.S1). Floodplain construction finished earlier than planned, and in March 2002, to control non-native species while other treatments were prepared, a temporary cover crop of sterile barley was sown with a seed blower at an undocumented rate in most but not all areas. Based on a local study (Stillwater Sciences 2001), native herbaceous species were chosen for the SEED treatment.

For organizational purposes and largely unrelated to environmental gradients, the site was divided into six management zones (Figure 2.2). Zones 2 and 4 received a different seed mix, as they were expected to be wetter due to (unrealized) irrigation plans and due to agricultural runoff observed in zone 4 (CADWR & CADFG 2003). In November 2002,

SEED areas were cross-ripped and smoothed, and on 6 January 2003, the mixes were aerially seeded at species-specific rates (Table 2.1) and then harrowed. Except for parts of zones 1 and 2, SEED areas were inoculated at 45 kg/ha with *Glomus intraradices* mycorrhizae bound in expanded mica. No specific justification was given for choosing these particular treatments, although there was a general interest in reducing costs by utilizing agricultural techniques (CADWR & CADFG 2003). Although trees were planted, there was no overstory at the monitoring transects except for an open canopy in zone 4 (Figure 2.2).

Vegetation Surveys

Herbaceous treatments were monitored in 0.25 m² plots spaced every 5 m along 45 m long transects established by California Department of Water Resource (CADWR) staff (Figure 2.2). In September 2002, after the BAR treatment, 24 transects were established, surveyed by CADWR staff, and never resurveyed. In 2003, after the SEED and MYCO treatments, 44 permanent transects were established. Both the 2002 and the permanent transects were spread across all zones except zone 5. Most permanent transects were monumented and thus easily relocated, and the remainder were relocated each time they were visited using a global positioning system with an estimated precision of 1 m. These permanent transects were surveyed by CADWR staff in July 2003, June 2004, and September 2005. We resurveyed a selection of the permanent transects in July 2008 and September 2011 and added three transects in a nearby unrestored area. Zone 4 was not surveyed in 2008 or 2011, as visual cover estimates were unsuited to the vegetation height, and zone 3 was not surveyed in 2011 due to access problems. All plots on a transect had received identical treatment combinations. Transects were not designated based on any

specific environmental basis. Observers quantified both fresh and senesced vegetation cover and species composition. Flooding in 2005 and 2011 delayed surveys until late summer, confounding flooding and survey date (Figure 2.1).

Plant cover was classified by species into modified Daubenmire classes (<<1%, <1%, 1–5%, 5–25%, 25–50%, 50–75%, 75–100%). For analysis, classes were represented by their midpoints. Because of this and physical overlap, estimated total cover can exceed 100%. Congenerics that could not be reliably distinguished were aggregated to genus. Including the remaining unidentifiable specimens as separate species had little qualitative impact except to inflate species richness, and here we present only the results from analyses excluding them.

Species were classified as native or non-native (Calflora 2008) and by wetland indicator status (Lichvar 2012). Experts from CADWR provided wetland indicator statuses for species otherwise lacking such information. For our analyses, we distinguished sterile barley from other non-native species, and we defined SEED species by the mix applied in each zone. We calculated a plot-level cover-weighted wetland indicator value, assigning obligate wetland, facultative wetland, facultative, facultative upland, and upland species values of 5, 2.5, 0, -2.5, and -5 respectively.

Quantitative Analyses

We used non-metric multidimensional scaling (NMDS) and Bray-Curtis dissimilarities to identify species associations (Oksanen et al. 2012). To achieve convergence, we aggregated our observations to transects, but we left observations in different years distinct. We did not downweight rare species, nor did we transform percent cover. Here we present the best 2-axis NMDS results from 100 runs of up to 200 iterations, as additional axes

complicate visualization without affecting the interpretation. Transects were classified post hoc by treatment, year, zone, and flooding.

Using mixed-effects models, we separated the effects of the individual treatments from the treatment combinations and examined treatment effects in different years (Supporting Information; Bates et al. 2012). The cover response variables were total, native, non-native, barley, non-barley, SEED, non-SEED native, and non-SEED cover (%), the diversity (Shannon's H) response variables were total, non-barley, and non-SEED diversity, and the species richness response variables were total, non-barley, and non-SEED richness. Response variables including or excluding SEED species were calculated based upon the seed mix applied to each plot. We wanted to partition the effects of the individual treatments within each treatment combination. We also wanted to examine whether effects changed over time. Therefore, the fixed effects were the interactions between survey year (categorical) and whether a treatment was applied to the plot (indicator/dummy variable). Since BAR and SEED were expected to interact, we also included the three-way interactions between survey year, BAR, and SEED when sample sizes were sufficient for estimation (2003, 2004, and 2005). Survey year, zone, and transect, but not plot were treated as categorical random effects (Supporting Information). Effect size was measured as the coefficient value and 95% highest posterior density credible intervals were calculated using locally uniform priors. Although there are nuances between Bayesian credible intervals and frequentist confidence intervals (Clark 2007), for the purposes of this paper, they can be treated in an equivalent manner, and effects were deemed significant if the credible intervals did not span zero.

Seed supply limitation was assessed using similar but species-specific mixed-effects models. The response variables were the cover of each SEED species with more than 0.25% mean cover (Table 2.2). Fixed and random effects were the same as previously, except the SEED treatment was considered applied to a plot only if its seed mix included the corresponding species. Given that a species limited by seed supply leaves unoccupied establishment niches, a species was considered possibly seed supply limited if the SEED treatment significantly enhanced its cover in 2003, although this is confounded with any effects of ripping and harrowing.

Variation explained by each term was measured by r^2 (Ω_0^2 ; sensu Xu 2003). The minimal variance explained was calculated as the difference between the r^2 of the full model and the r^2 of the model lacking only that term, while maximal variance explained was calculated as the r^2 of the model consisting only of that term.

All analyses were conducted in R (R Core Team 2012) with the devEMF (Johnson 2015), lme4 (Bates et al. 2013), RCurl (Lang & CRAN 2012a), rgdal (Bivand et al. 2014), rjson (Couture-Beil 2013), vegan (Oksanen et al. 2013), and XML (Lang & CRAN 2012b) packages.

Results

Vegetation in most plots was sparse and moderately diverse (Table 2.3). Species composition varied greatly among plots, and the herbaceous community was largely structured (NMDS final stress 0.25) by wetland tendency (Figure 2.3), flooding (Figure 2.4), and SEED treatment (Figure 2.5), but not by distance from the river (Figure 2.3). Observations were loosely organized by year only until 2004 (Figure 2.S1), after which flooding determined community structure, although sampling date was confounded with

flooding. Composition was largely independent of zone, except for the perennially wet zone 4. The BAR transects were distinguishable from non-BAR transects only in 2002, while the SEED treatment only influenced community structure until 2004 and MYCO transects showed no additional similarity beyond having all been subjected to the SEED treatment. Notably, native perennial grasses were never common, even in SEED areas.

Plant assemblages sorted along a gradient from those dominated by wetland species to those dominated by upland species. Wetland species were common following floods and in the artificially wetted zone 4. Other than *Cynodon dactylon*, there was little overlap between the flood community, which was dominated by non-native species such as *Lythrum hyssopifolium* and *Polypogon monspeliensis*, and the zone 4 community, which was dominated by a mix of native freshwater emergent wetland species including several from the *Cyperus*, *Eleocharis*, and *Juncus* genera as well as the generalist SEED species *Acmispon americanus* var. *americanus* and non-natives such as *Echinochloa crus-galli* and *Melilotus albus* (Table 2.4). The unrestored transects were dominated by upland species, primarily non-native annual grassland species of the *Avena*, *Bromus*, and *Erodium* genera, and were not flooded during this study. The restored floodplain outside of zone 4 and outside of flood years was mostly dominated by upland species, and observations could be divided among those observations in 2002, after floodplain reconstruction and the BAR treatment but before the other revegetation treatments, those observations exhibiting a transient SEED community (i.e., SEED transects in 2003 and 2004), and those observations exhibiting the “non-flood community” (i.e., both non-SEED transects after 2002 and SEED transects in 2008). In 2002, barley was dominant, along with *Acmispon americanus* var. *americanus* and a few native species that were only common then. The SEED transient was

dominated by the SEED species *Acmispon americanus* var. *americanus*, *Festuca microstachys*, and *Lupinus bicolor* along with remnant barley and a number of non-native species (not seeded), while non-SEED native species were uncommon. Upland species dominated SEED transient transects, regardless of seed mix, partly because irrigation was never implemented. By contrast, the non-flood community was mostly dominated by non-native species such as *Brassica nigra* and various *Erodium* species, along with some SEED species such as *Acmispon americanus* var. *americanus* and *Festuca microstachys*.

The treatments had few significant effects. The variance explained by the mixed-effects models (r^2) was 56% for total cover, 37% for total richness, and 26% for total diversity, but random effects explained more than the treatments, which explained little individually or together (Table 2.5). Although the treatments did have significant effects (Figure 2.6), some were expected due to chance alone given the number of mixed-effects models examined, and we focus here on interpretable effects. Relatively little barley emerged, and its cover diminished into statistical insignificance by 2004. Other than increasing the cover of barley itself, the BAR treatment did not significantly affect any other features in 2002, and while barley increased overall richness and diversity in 2003, it did not significantly affect the richness or diversity of non-barley species. The SEED species attained significantly higher cover in SEED plots in 2003 and even more so in 2004, with corresponding significant decreases in the cover of non-SEED species in both years, a significant decrease in the richness of non-SEED species in 2004, and a significant decrease in non-native cover in 2004. There were no interpretable significant effects of the MYCO treatment or the interaction between the BAR and SEED treatments. In other words, there were few treatment effects beyond short-term increases in the cover of BAR and SEED species.

The SEED treatment had few noticeable effects. Of the 13 SEED species, only *Acmispon americanus* var. *americanus*, *Artemisia douglasiana*, *Festuca microstachys*, and *Lupinus bicolor* attained more than 0.25% mean cover added across all plots and years. None of these 4 species were significantly affected by the SEED treatment in 2003 (Figure 2.7), and all were found in non-SEED plots (4.5% cover of SEED species expected in a typical 2003 control plot). However, the SEED treatment significantly increased the cover of *Artemisia douglasiana* and *Festuca microstachys* in 2004, while fewer SEED species were found in non-SEED plots (0.5% cover expected in a typical 2004 control plot). Only *Artemisia douglasiana* demonstrated interpretable significant effects of the SEED treatment in later years.

Discussion

Nearly a decade after restoration, the floodplain vegetation of the Robinson Reach of the Merced River remained far from expectations for riparian floodplains (Conard et al. 1977). Ground cover was relatively sparse and patchy, with little similarity among plots. Common species were disturbance-adapted, largely non-native, and habitat generalists. Restoration treatments were largely ineffective at either reducing non-native species or promoting native species. Given these results, we suggest that restoration managers in similar systems consider a different approach to managing the recovery of the herbaceous community that entails planning for natural regeneration, directing remedial attention to those species, areas, and treatments that are likely to be more effective and persistent, and only controlling especially undesirable non-native species.

The BAR treatment did not noticeably inhibit the establishment of non-native species as it was designed to do, partly due to the modest amounts of barley that emerged, partly due to

treatment timing, and partly due to the inherent limitations of using cover crops for weed control. Successful agricultural cover crops satisfy a Roshambo criterion; the cover crop must suppress the weeds that suppress the economic crop while still giving way to the economic crop. This can be difficult to accomplish in restoration sites (Perry & Galatowitsch 2003), especially given the diversity of restoration seed mixes and plantings. Furthermore, cover crops are often plowed under prior to or soon after seed set and the economic crop immediately planted, whereas the extended period between the BAR and SEED treatments offered opportunities for weeds to establish. Additionally, cover crops may suppress desirable species emerging from residual seed banks, they may require tending to achieve meaningful cover, they may deplete shallow soil moisture and inhibit subsequent restoration efforts, and their seed batches may be contaminated with undesirable species (Keeley 2006).

Although the SEED treatment briefly promoted native species, the performance of individual species varied greatly, and it ultimately had little long-term effect. Direct seeding is often unpredictable for several reasons (e.g., Wolden & Stromberg 1997). Regional prevalence is not a sufficient indication of local suitability, and the extremely gravelly coarse sand on the floodplain was a poor substrate for most of the SEED species (Bahre & Whitlow 1982), leading to only trivial amounts of 9 of the 13 SEED species. Similarly, neither *Stipa cernua* nor *Stipa pulchra* is flood tolerant, and *Elymus triticoides* prefers moist soils (Caltrans 2001). Although there are guides for some species (e.g., Schmidt & Greenberg 2012), the substrate and moisture requirements of many species remain undocumented, precluding more narrowly targeted treatments. The remaining 4 non-trivial SEED species all colonized without assistance, indicating seed supply did not limit their on-

site presence. None of these non-trivial species were significantly more abundant in SEED plots in 2003, suggesting that seed supply did not limit their abundance. However, *Artemisia douglasiana* achieved significantly higher cover in SEED plots in 2004, 2005, and 2008, consistent with sustained growth from low densities of individuals that established in 2003. The annual *Festuca microstachys* also achieved significantly higher cover in 2004, but its cover was reduced by flooding in 2005. Finally, secondary dispersal of unincorporated seed may have contributed to the observed results, and the effects of seeding were also confounded with those of ripping and harrowing. In short, a detailed understanding of species habitat preferences, local seed supply, and flood responses could facilitate the design of effective and persistent restoration treatments.

Mycorrhizal inoculation had no measureable effect. The mycorrhizae may have failed to establish, perhaps due to an inhospitable site or inhibition by root exudates (Schreiner & Koide 1993). Also, natural establishment of mycorrhizal relationships in uninoculated areas may have masked treatment effects. We found no studies examining whether or not *Glomus intraradices* associates with any of the seeded species, but early successional plants often associate weakly with mycorrhizal fungi (Francis & Read 1995).

We did not observe the coherent coupling of landforms and vegetation types expected for this setting based on published gradient models (e.g., Conard et al. 1977). With the exception of zone 4, surveyed areas appeared hydrologically homogeneous. Floodplain vegetation patterns are influenced by shallow groundwater (Stromberg et al. 1996), but groundwater in the surveyed areas was generally deep (Supporting Information) and soils very well drained. Relief on the constructed floodplain was so low that floods usually inundated the entire floodplain, rendering flood-driven patch dynamics largely irrelevant. In

other words, despite the relatively large width of the reconstructed floodplain (300–500 m), surveyed areas outside of zone 4 comprised a single landform. Zone 4 did comprise a distinct landform supporting distinct wetland vegetation produced by water entering the zone from adjacent irrigated cropland. Finally, the transects were established to monitor the revegetation treatments and did not include perennial wetlands within the immediate channel margin or perennial uplands situated further upslope (pers. obs.).

Most of the restored floodplain experienced multiple years of upland conditions punctuated by several months of inundation, favoring common and frequently non-native ruderal species. Flood-adapted species such as *Lythrum hyssopifolium*, *Polygonum aviculare* ssp. *depressum*, and *Polypogon monspeliensis* proliferated briefly following prolonged inundation, but did not persist across intervening drought years. Droughty floodplain soils exerted a strong influence excluding wetland species in favor of relatively drought-tolerant upland species such as *Acmispon americanus* var. *americanus*, *Brassica nigra*, and *Erodium cicutarium*, which were in turn poorly adapted to prolonged flooding. As a result, floodplain vegetation at the site alternated between a wetland flood-year community and an upland non-flood-year community, both of which were dominated by non-native species.

This relatively long term monitoring dataset from the Robinson Reach of the Merced River suggests that, in the absence of further modifications to the biophysical environment, the herbaceous community would continue to be dominated by ruderals. The few native perennials that established did so in only small quantities, even when seeded, indicating inhibition by an environmental filter and not seed supply limitation. Admittedly, treatments were only applied once, and species may possibly recruit episodically and might have done

better had the treatments been applied in some other year. Similarly, other untested and unobserved species might be both limited by seed supply but capable of establishing self-sufficient populations. Furthermore, species exhibiting commensal or facilitative relationships, such as canopy-dependence (Moore et al. 2011), may be able to establish at later stages of floodplain succession.

Is there value in restoring native ruderal species? In Mediterranean climates, annuals are sensitive to the timing of winter precipitation (Bartolome 1987) as well as the variations in flood impact and timing typical of riparian habitats (Bagstad et al. 2005). Species selection is challenging, as it is uncertain which species might flourish at the time restoration treatments are to be implemented. Furthermore, some species did not require assistance from treatments, while others required reapplication of treatments following flooding. Seeding is particularly questionable when nearby seed sources exist, as ruderal species are generally well dispersed, and seeding is also questionable in disturbance-prone environments when nearby seed sources do not exist, as ruderal species often depend on such dispersal to re-establish following disturbance. Given the unpredictability of riparian habitats, it is difficult to ensure the effectiveness of treatments aimed at native ruderals. Nonetheless, these species tend to be well-adapted for variable environments, and it may be sufficient to simply provide local introductions (Mitsch & Wilson 1996).

Much of the restored Merced floodplain exhibited wide interannual variations in hydroperiod that restricted the herbaceous community and the range of effective restoration treatments. Most years were characterized by dry Mediterranean summers exacerbated by deep groundwater and coarse, droughty soils, which stood in contrast with occasional years of prolonged flooding into summer. This drought/flood bimodality appeared to restrict the

herbaceous community to primarily ruderals, many of which are unlikely to benefit from restoration treatments such as seeding. Similarly, disturbance-prone environments tend to be inherently invasible, and it may be most effective to restrict control efforts to noxious or otherwise exceptionally undesirable invaders (e.g., *Centaurea solstitialis*). Given the natural dispersal and recruitment capabilities of the ruderal species that dominated the floodplain and the apparent lack of suitability of other desirable riparian species to this particular riparian landform, we suggest deferring active revegetation under these conditions and relying instead on spontaneous revegetation, especially for ruderal species. Scarce restoration resources might be better spent identifying or creating areas more conducive to longer-lived riparian species, such as more typical habitats with at least a superficial layer of fine sediment, low elevation point bars, and backwater sloughs, as well as areas with a more persistent upland character where standard upland restoration methods can be applied.

Conclusion

The surveyed portion of the reconstructed Merced floodplain consisted largely of a single landform that toggled between periodic prolonged flooding and multiple years of semi-arid Mediterranean summers exacerbated by exceptionally droughty soils and deep groundwater. Common species were ruderal, with non-native grasses typical of annual grassland as well as wetland species and native forbs. This community varied greatly, most obviously in response to flooding, and only temporarily due to seeding. Sowing barley was ineffective and sowing native species produced only a brief pulse of increased cover by some seeded species. Mycorrhizal inoculation had little effect. When planning restorations for comparable ruderal-dominated floodplains exhibiting a severe dichotomy between flood and non-flood years, we suggest focusing on promoting natural regeneration and control of

specific exceptionally disruptive non-native species. Identification of those areas likely to support or shelter long-lived native perennial species may be the key to maximizing the success of restorative activities in such floodplains.

Implications for Practice

- In some Mediterranean-climate floodplain habitats associated with regulated rivers, an unusually severe combination of flood and drought stress favors weedy species that can often reach restored sites and flourish unassisted. This setting also provides invasion opportunities that can undo one-time non-native control efforts.
- Restoration effort may be better spent locating or creating more consistent habitats, such as persistent wetlands that support slower-growing and longer-lived species as well as adjacent areas with more consistently upland characteristics.

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Tables

Table 2.1. Native species sown in the SEED treatment with seed source and application rate (kg/ha of pure live seed). A separate mix was used for management zones that were expected to be wetter.

Scientific Name	Common Name	Source	Duration	Rate
dry zones (1, 3, 5, and 6)				
<i>Achillea millefolium</i>	Yarrow	Sierra N.F.	Perennial	1.12
<i>Acmispon americanus</i> var. <i>americanus</i>	Spanish lotus	Plumas N.F.	Annual	1.12
<i>Artemisia douglasiana</i>	Mugwort	Delta	Perennial	0.28
<i>Elymus triticoides</i>	Creeping wild rye	Fresno County	Perennial	2.25
<i>Festuca microstachys</i>	Small fescue	Sierra N.F.	Annual	5.62
<i>Melica californica</i>	California melic	Carrizo Plain	Perennial	1.12
<i>Stipa cernua</i>	Nodding needlegrass	Bakersfield	Perennial	2.25
<i>Stipa pulchra</i>	Purple needlegrass	Lincoln	Perennial	2.25
wet zones (2 and 4)				
<i>Achillea millefolium</i>	Yarrow	Sierra N.F.	Perennial	2.93
<i>Artemisia douglasiana</i>	Mugwort	Delta	Perennial	0.40
<i>Carex barbarae</i>	Barbara sedge	Mariposa	Perennial	0.40
<i>Elymus triticoides</i>	Creeping wild rye	Fresno County	Perennial	2.93
<i>Festuca microstachys</i>	Small fescue	Sierra N.F.	Annual	2.93
<i>Hordeum brachyantherum</i>	Meadow barley	Solano County	Perennial	5.86
<i>Lupinus bicolor</i>	Miniature lupine	Delta	Annual	1.42
<i>Muhlenbergia rigens</i>	Deer grass	Chico	Perennial	0.40
<i>Trifolium obtusiflorum</i>	Clammy clover	Modesto	Annual	2.93

Table 2.2. Regression terms. Interactions are indicated by ×. All fixed effects and all random effects were categorical. Models contained all fixed effects and all random effects, although SEED fixed effects were adjusted for species-specific responses to reflect the seed mixes containing those species.

Response variables	Total cover (%), native cover (%), non-native cover (%), barley cover (%), non-barley cover (%), SEED cover (%), non-SEED native cover (%), non-SEED cover (%), total diversity (H), non-barley diversity (H), non-SEED diversity (H), total species richness, non-barley richness, non-SEED richness, cover of <i>Artemisia douglasiana</i> (%), cover of <i>Acmispon americanus</i> var. <i>americanus</i> (%), cover of <i>Lupinus bicolor</i> (%), cover of <i>Festuca microstachys</i> (%)
Fixed effects	BAR×survey year, SEED×survey year, BAR×SEED×survey year, MYCO×survey year
Random effects	Survey year, management zone, transect

Table 2.3. Summary of plot-level monitoring survey data with total percent cover, total species richness, total diversity as Shannon’s H, and Bray-Curtis similarity. Values are mean \pm standard error for the given year or zone, except for similarity, for which values are the mean pairwise similarity within the given year or zone, and for which standard error is non-trivial.

	Cover (%)	Richness	Diversity	Similarity
Year				
2002	24 \pm 2	3.25 \pm 0.15	0.65 \pm 0.03	0.11
2003	54 \pm 2	5.29 \pm 0.08	1.09 \pm 0.02	0.13
2004	58 \pm 1	4.91 \pm 0.10	1.02 \pm 0.02	0.12
2005	36 \pm 2	3.68 \pm 0.11	0.87 \pm 0.03	0.06
2008	33 \pm 2	6.92 \pm 0.16	1.24 \pm 0.03	0.17
2011	25 \pm 2	4.85 \pm 0.17	0.99 \pm 0.03	0.06
Zone				
1	20 \pm 1	4.36 \pm 0.13	0.96 \pm 0.03	0.09
2	39 \pm 1	4.52 \pm 0.10	0.93 \pm 0.02	0.06
3	52 \pm 2	4.73 \pm 0.11	0.97 \pm 0.02	0.08
4	73 \pm 2	5.80 \pm 0.15	1.14 \pm 0.03	0.11
6	36 \pm 1	4.42 \pm 0.12	0.92 \pm 0.03	0.06
Unrestored	40 \pm 4	6.40 \pm 0.31	1.20 \pm 0.07	0.12
Overall	42 \pm 1	4.74 \pm 0.05	0.98 \pm 0.01	0.05

Table 2.4. Top species by total percent cover in each NMDS group. Native species are bolded and SEED species and barley are also underlined. Superscripts indicate annual (a), biennial (b), or perennial (p) duration. Genera, consisting of species confounded in the field, are bolded if identified species were predominantly native and are similarly assigned a duration only if shared by nearly all identified species, but are underlined if they contained any SEED species. Full species lists are given in Table 2.S2.

zone 4	flood	non-flood	SEED transient	unrestored	2002
<i>Cynodon dactylon</i> ^p	<i>Polypogon monspeliensis</i> ^a	<u><i>Acmispon americanus</i></u> <u>var. <i>americanus</i></u> ^a	<u><i>Festuca microstachys</i></u> ^a	<i>Bromus diandrus</i> ^a	<u><i>Hordeum vulgare</i></u> ^a
<i>Melilotus albus</i> ^{ab}	<i>Lythrum hyssopifolium</i> ^{ap}	<i>Erodium</i> spp. ^a	<u><i>Acmispon americanus</i></u> <u>var. <i>americanus</i></u> ^a	<u><i>Lupinus</i> spp.</u>	<i>Cyperus</i> spp. ^p
<u><i>Cyperus</i> spp.</u> ^p	<i>Polygonum aviculare</i> ssp. <i>depressum</i> ^{ap}	<u><i>Trifolium</i> spp.</u> ^a	<u><i>Hordeum vulgare</i></u> ^a	<i>Bromus hordeaceus</i> ^a	<i>Persicaria hydro Piperoides</i> ^p
<i>Echinochloa crus-galli</i> ^a	<i>Cynodon dactylon</i> ^p	<i>Brassica nigra</i> ^a	<i>Brassica nigra</i> ^a	<i>Hypochaeris glabra</i> ^a	<i>Echinochloa crus-galli</i> ^a
<u><i>Acmispon americanus</i></u> <u>var. <i>americanus</i></u> ^a	<i>Brassica nigra</i> ^a	<i>Spergularia bocconi</i> ^a	<u><i>Lupinus</i> spp.</u>	<i>Erodium</i> spp. ^a	<i>Chenopodium album</i> ^a
<u><i>Eleocharis</i> spp.</u> ^p	<i>Festuca perennis</i> ^{ap}	<i>Melilotus albus</i> ^{ab}	<i>Melilotus albus</i> ^{ab}	<i>Avena</i> spp. ^a	<i>Croton setigerus</i> ^a
<i>Paspalum dilatatum</i> ^p	<i>Euphorbia maculata</i> ^a	<u><i>Lupinus</i> spp.</u>	<i>Vicia sativa</i> ^a	<i>Eschscholzia californica</i> ^{ap}	<u><i>Acmispon americanus</i></u> <u>var. <i>americanus</i></u> ^a
<i>Sorghum halepense</i> ^p	<i>Xanthium strumarium</i> ^a	<i>Festuca myuros</i> ^a	<i>Centaurea solstitialis</i> ^a	<i>Cucurbita palmata</i> ^{ap}	<i>Brassica nigra</i> ^a
<i>Persicaria hydro Piperoides</i> ^p	<i>Spergularia bocconi</i> ^a	<i>Polypogon monspeliensis</i> ^a	<i>Erodium</i> spp. ^a	<i>Croton setigerus</i> ^a	<i>Kickxia elatine</i> ^p
<i>Juncus</i> spp.	<i>Centaurea solstitialis</i> ^a	<u><i>Festuca microstachys</i></u> ^a	<u><i>Artemisia douglasiana</i></u> ^p	<i>Festuca octoflora</i> ^a	<i>Melilotus albus</i> ^{ab}

Table 2.5. Variation explained (r^2) by the full models and the range of variation explained by subsets of terms.

Response Terms	Total cover	Richness (S)	Diversity (H)
Treatments	0.03–0.20	0.02–0.14	0.02–0.09
Seeding	0.01–0.08	0.00–0.07	0.01–0.04
Barley	0.01–0.13	0.01–0.12	0.01–0.08
Mycorrhizae	0.00–0.08	0.00–0.05	0.00–0.02
Random effects	0.36–0.53	0.23–0.35	0.17–0.24
Full model	0.56	0.37	0.26

Figures

Figure 2.1. Restoration timeline and hydrograph.

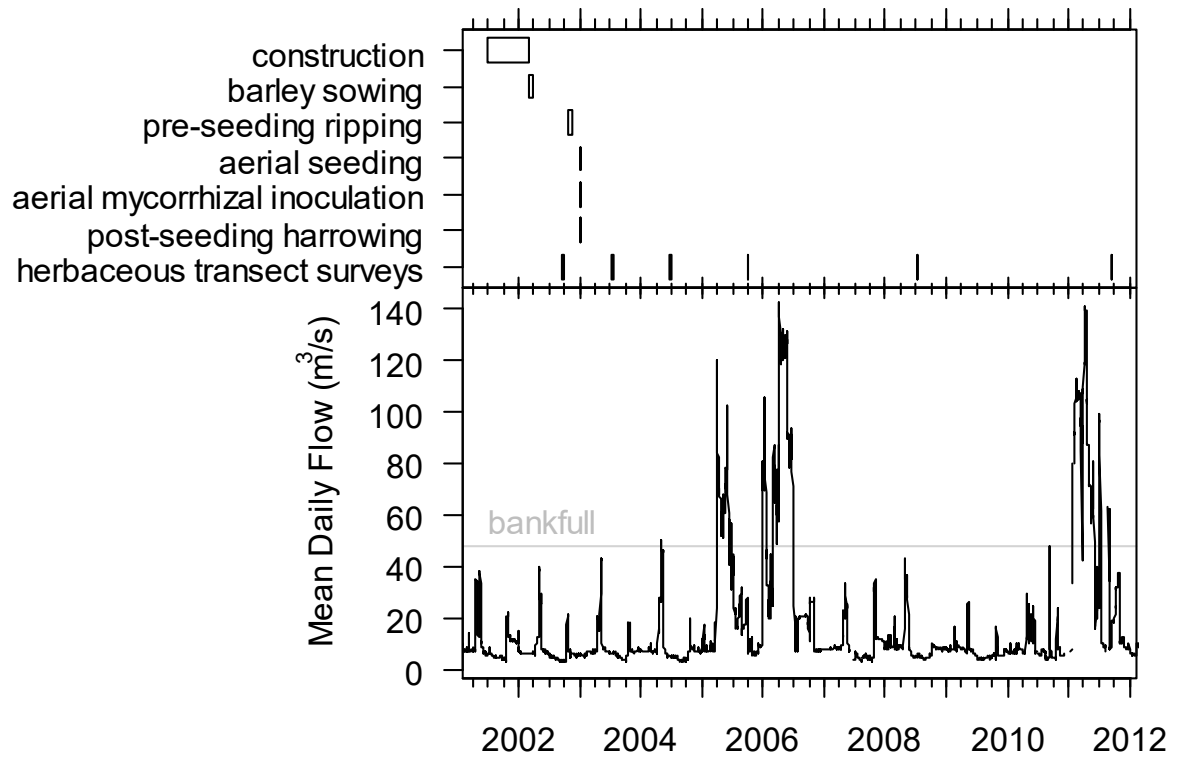


Figure 2.2. Restoration site and a) management zones and 2006 imagery, b) 2002 control transects, c) 2002 transects subjected to the BAR treatment, d) permanent control and unrestored transects, e) permanent transects subjected to the BAR treatment, f) permanent transects subjected to the SEED treatment, and g) permanent transects subjected to the MYCO treatment. In panels b–f, zones and transects not subject to the treatment are underlain for reference.

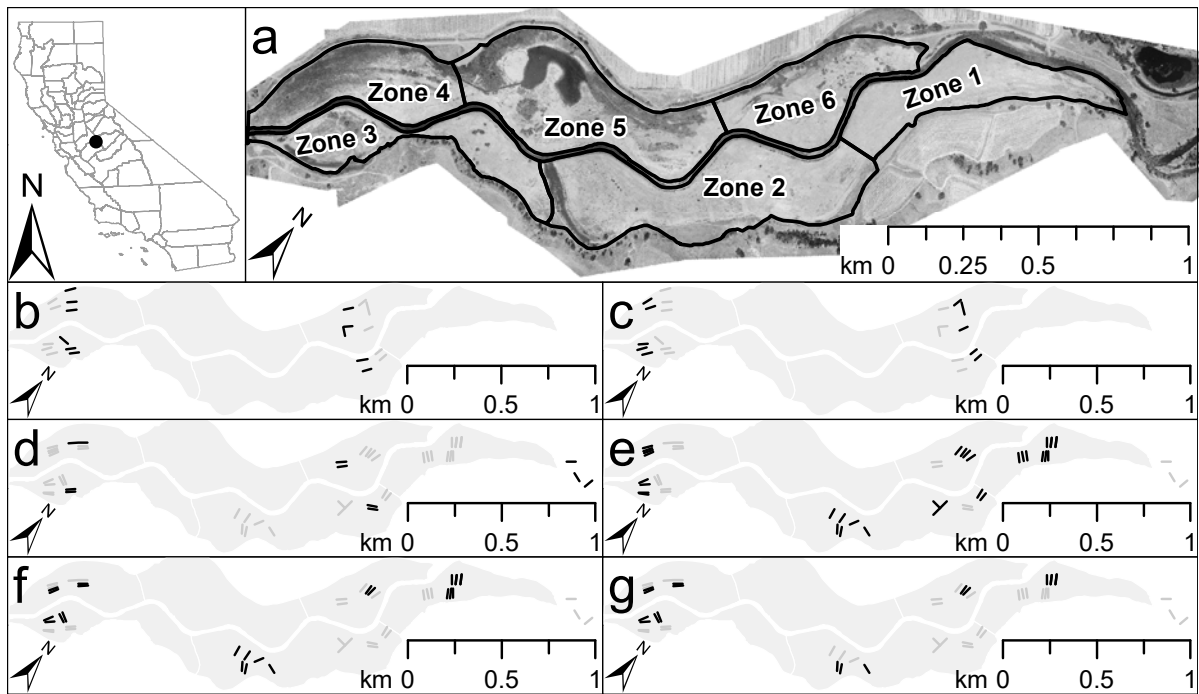


Figure 2.3. Observations of survey transects in NMDS ordination space, shaded according to transect-level wetland status indicator and distance to the river.

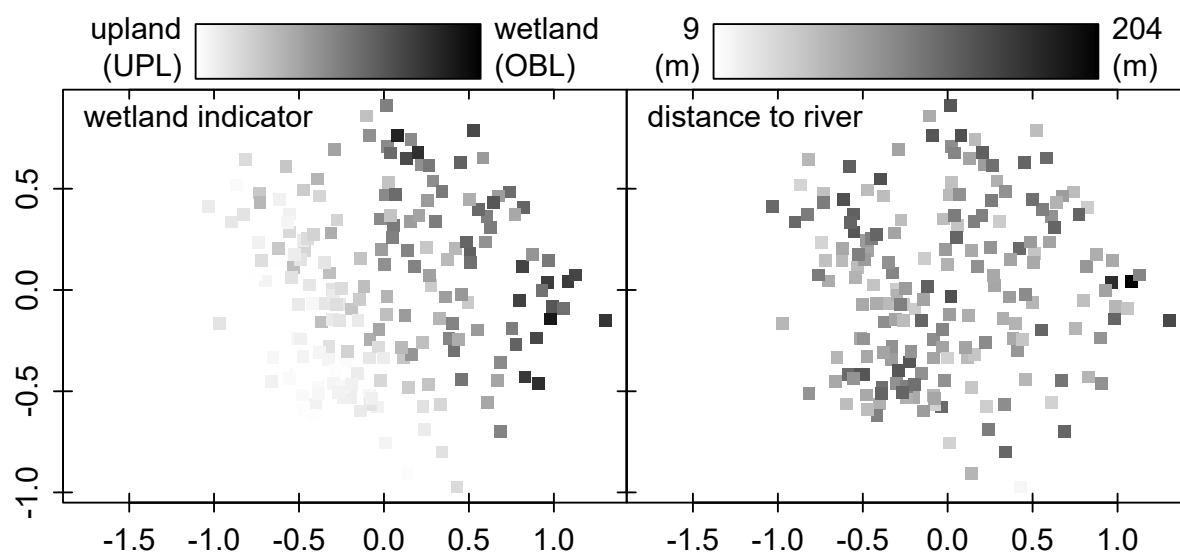


Figure 2.4. Observations of survey transects in NMDS ordination space showing post hoc interpreted clusters. Cluster points are emphasized (●), while other observations are deemphasized but retained for reference (○). Reference unrestored transects, transects in the perennially wetted zone 4, and observations in the midst of restoration activities in 2002 were all distinct. The remaining observations were partitioned among a SEED transient comprising SEED transects in 2003 and 2004, transects during flood years (2005 and 2011), and non-flood transects composed of non-SEED transects and transects in 2008.

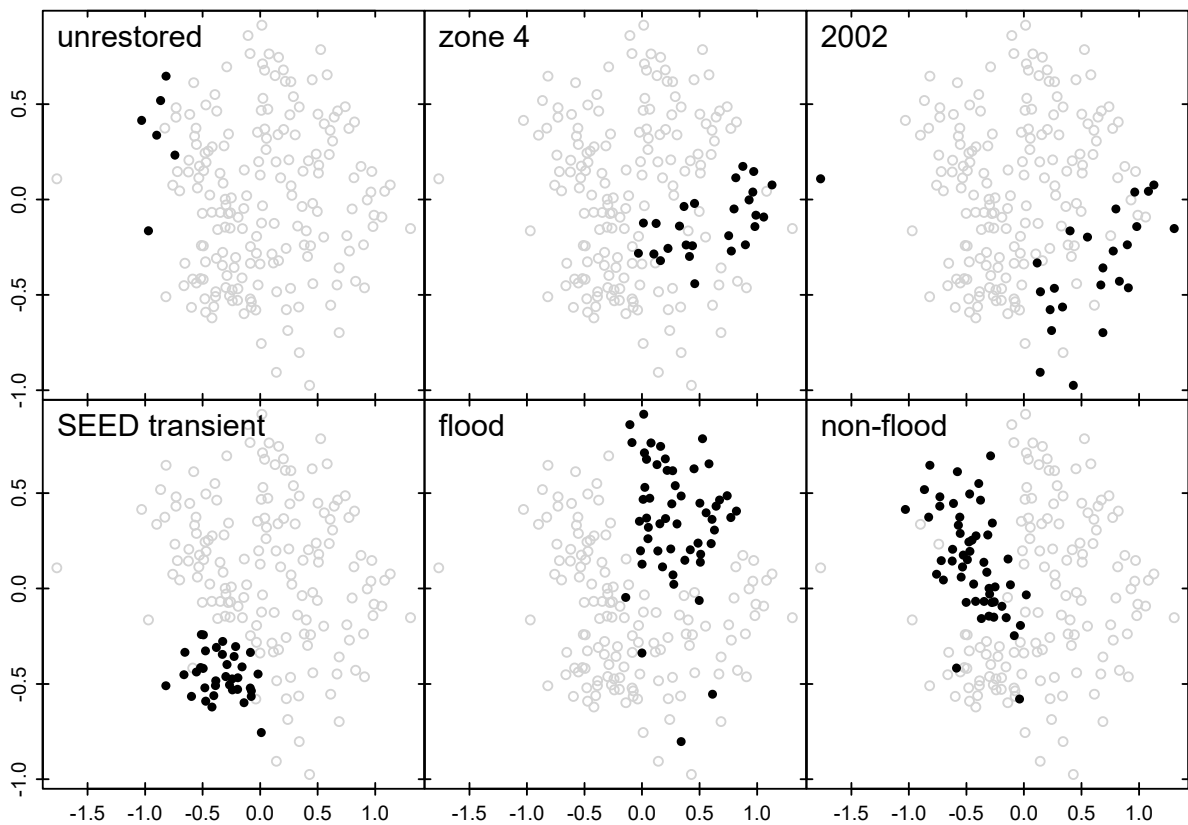


Figure 2.5. Observations of survey transects on the restored floodplain in NMDS ordination space, highlighting treatments applied (rows) and stratified by year (columns) and whether the observation was made in a zone that received a dry seed mix (●), in zone 2, which was dry despite receiving a wet seed mix (○), or in the artificially wetted zone 4, which received a wet seed mix (×). The control treatment combination (CON) is shown alongside the component treatments, SEED, BAR, and MYCO. Further details about the treatments and the combinations in which they were applied are presented in the methods. In each year, transects that did not receive the indicated treatment are underlain in grey for reference.

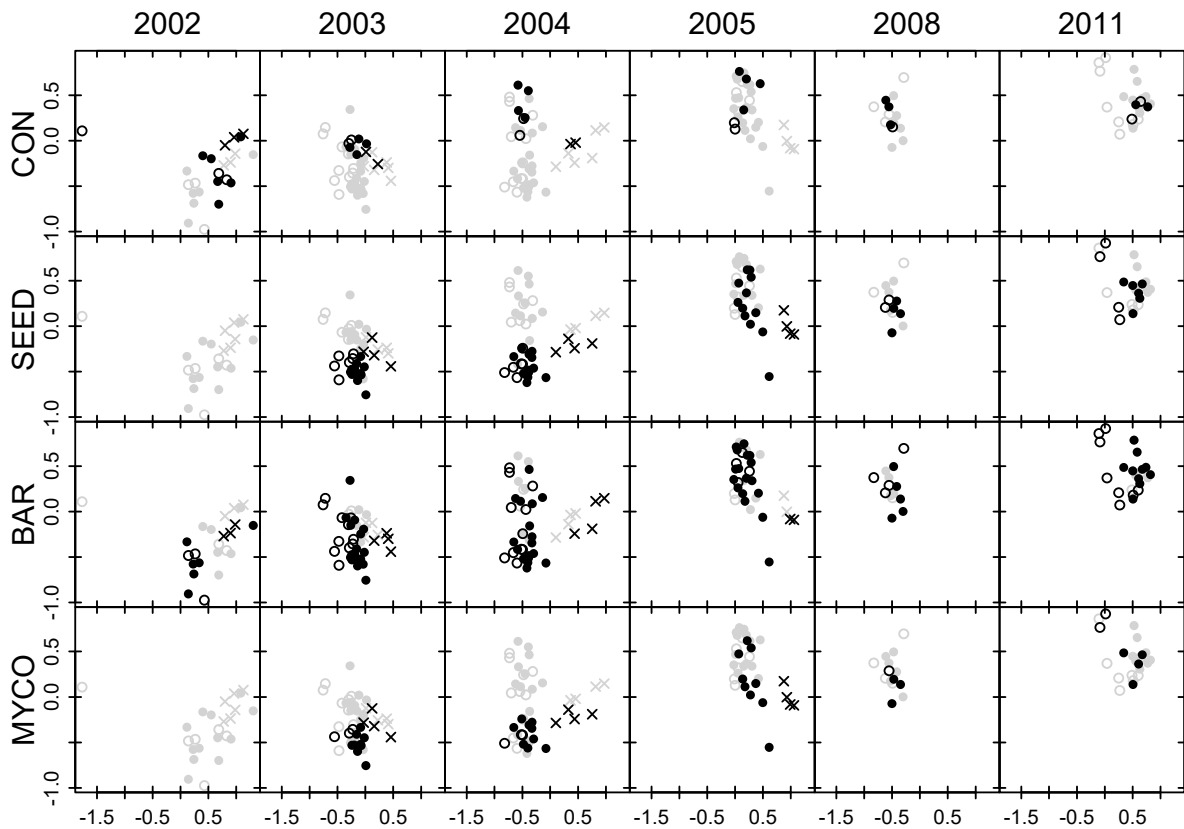


Figure 2.6. Treatment effects on aggregated percent cover, species richness, and diversity measures. Each bar indicates the effect size of a treatment, noted in the top left of each row, on a response variable, indicated by the group of bars and panel, in a given year, indicated by the bar color. For consistency, the number of bars within each group and their order is always the same. For example, the bottom-left-most bar is the effect of the mycorrhizal inoculation on total percent cover in 2003. Error bars are 95% highest posterior density credible intervals.

Treatment effect in: ■ 2002 ■ 2003 ■ 2004 ■ 2005 ■ 2008 ■ 2011

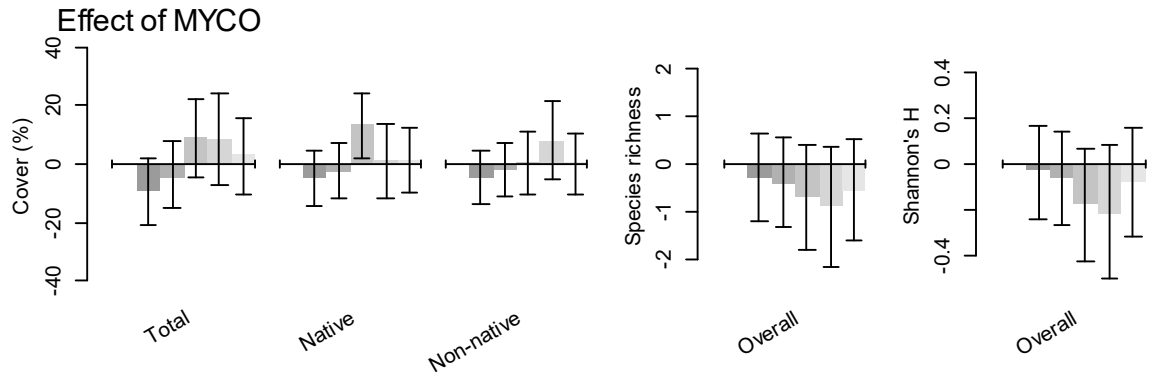
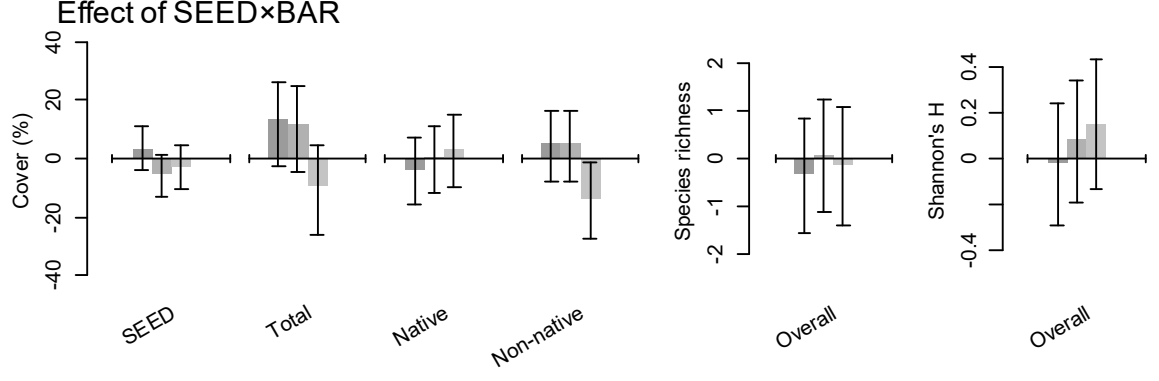
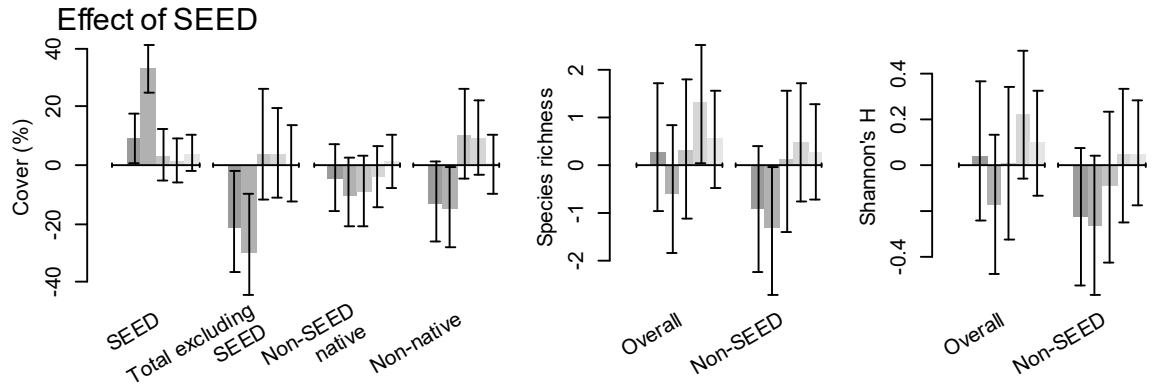
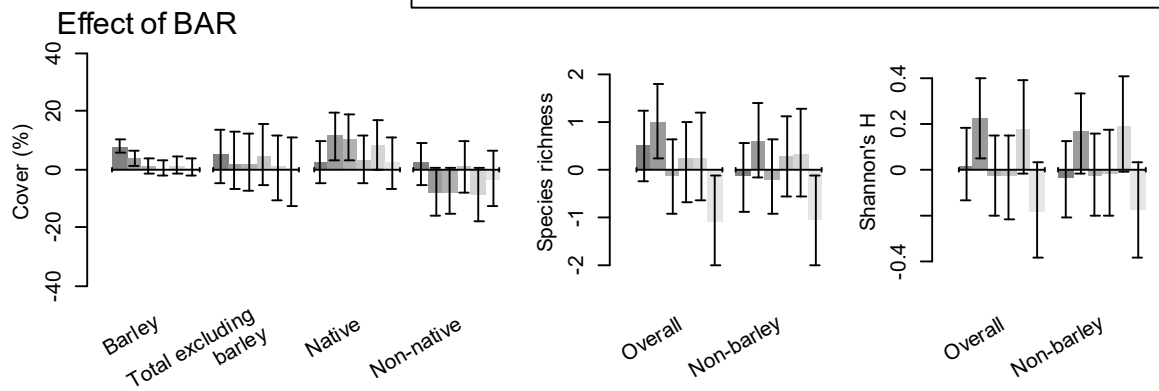
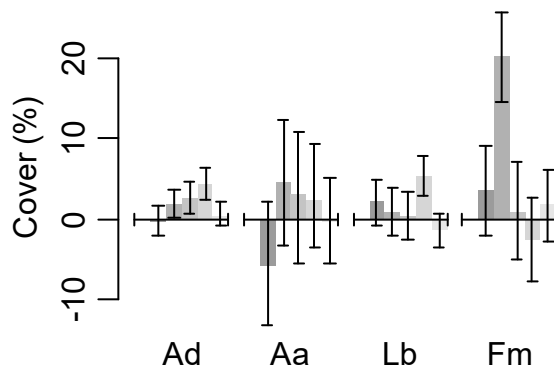


Figure 2.7. Effect of the SEED treatment on the percent cover of SEED species with more than 0.25% mean cover, which were *Artemisia douglasiana* (Ad), *Acmispon americanus* var. *americanus* (Aa), *Lupinus bicolor* (Lb), and *Festuca microstachys* (Fm). Each bar in a group corresponds in order from left to right to the effect in 2003, 2004, 2005, 2008, and 2011, with shading and a space left for 2002 for consistency with Figure 2.6. Error bars are 95% highest posterior density credible intervals.



Supporting Information

Mixed-effects Models

We used mixed-effects models because our data are unbalanced (Table 2.S3) and because the survey plots are organized along transects which are themselves organized within zones. The treatment×survey year fixed effects distinguish treatment effects in different years. We used the nested spatial random effects (transects and zones) to represent correlations between plots on the same transect and between transects within the same zone. Similarly, we used a temporal random effect (survey year) to represent correlations between plots observed at the same time. This model design is similar to having separate regressions for each year, except spatial random effects are pooled.

As an example, we present the model for total cover:

$$r_{ijk\ell} = \alpha + \sum_y (\beta_{By}B_{ij\ell y} + \beta_{Sy}S_{ij\ell y} + \beta_{My}M_{ij\ell y} + \beta_{BSy}B_{ij\ell y}S_{ij\ell y}) + \zeta_i + \tau_{ij} + \gamma_\ell + \varepsilon_{ijk\ell},$$

where the response variable $r_{ijk\ell}$ is the total cover observed during survey year ℓ in plot k on transect j in zone i , α is the regression intercept, $B_{ij\ell y}$, $S_{ij\ell y}$, and $M_{ij\ell y}$ are dummy variables indicating whether survey year y is equivalent to survey year ℓ and also whether transect j in zone i was subject to the BAR, SEED, and MYCO treatments respectively, β_{By} , β_{Sy} , and β_{My} are their corresponding fixed effect coefficients and β_{BSy} is the fixed effect coefficient for the BAR×SEED interaction, ζ_i is the random effect of plots observed in zone i , τ_{ij} is the random effect of plots observed on transect j in zone i , γ_ℓ is the random effect of plots observed during survey year ℓ , and $\varepsilon_{ijk\ell}$ is the residual error. The random effects and the individual error are normally distributed with variances σ_ζ , σ_τ , σ_γ , and σ_ε :

$$\zeta_i \sim N(0, \sigma_\zeta)$$

$$\tau_{ij} \sim N(0, \sigma_\tau)$$

$$y_\ell \sim N(0, \sigma_y)$$

$$\varepsilon_{ijkl} \sim N(0, \sigma_\varepsilon).$$

Because the SEED and MYCO treatments had not been implemented in 2002, there are naturally no corresponding $\beta_{Sy}S_{ij\ell y}$, $\beta_{My}M_{ij\ell y}$, or $\beta_{BSy}B_{ij\ell y}S_{ij\ell y}$ terms for 2002. Sample sizes were only sufficient to estimate the $\beta_{BSy}B_{ij\ell y}S_{ij\ell y}$ terms in 2003, 2004, and 2005.

Except for the species-specific models, all mixed models share this same structure and vary only in the response variable r_{ijkl} . In the species-specific models, the dummy variable $S_{ij\ell y}$ has a slightly different meaning and instead indicates whether transect j in zone i was treated with a native seed mix containing the particular species of interest.

Spatial Organization

We examined the spatial organization of the herbaceous community at the scale of individual plots, transects of plots, and zones of transects. To examine the effect of spatial scale, we compared additional nested models, one with additional plot-level random effects and another without transect-level random effects. Model comparison utilized marginal Akaike Information Criterion (mAIC), which is appropriate when comparing population-level parameters and random effects represent correlations in the residuals (Vaida & Blanchard 2005). Although mAIC is biased, there is no simple correction (Grevén & Kneib 2010).

In the mixed-effects models, the transect scale best explained the variation in richness and diversity, while the plot scale better explained the variation in total percent cover (Table

2.S4). Models with transect-level random effects fit significantly better than those with only zone-level random effects. In the richness and diversity models, plot-level random effects did not improve fit. Although including plot-level random effects better explained the variation in total percent cover, the improvement was not significant. For convenience, we presented only results from models with transect-level random effects.

We tested model residuals for spatial autocorrelation using Moran's I. With the inclusion of transect-level random effects, we found no significant spatial autocorrelation in the residuals of any model, despite such in models with only zone-level random effects.

Groundwater

Thirty-five groundwater monitoring piezometers ranging from 2.4–4.6 m in length were established as part of the restoration monitoring activities in 2002 (CADWR & CADFG 2003). In 2010, only 29 piezometers could be relocated, none of which were situated in zone 4, and of these, 3 piezometers were both situated in zone 5 relatively far from any herbaceous community survey transects and also situated near an off-channel pond that locally elevated the groundwater table, and so only data from the remaining 26 piezometers are presented here. The piezometers were sampled generally biweekly from April through October, during which time the river experienced several elevated but not overbank flows. Out of 312 measurements, piezometers were completely dry 215 times, and for the sake of analysis, the groundwater table was assumed to be at the bottom of the piezometer. In other words, the mean depth to groundwater is underestimated and biased shallow, with deeper estimates more strongly biased. Mean depths to groundwater ranged from roughly 1 m to more than 3 m, and shallower groundwater measurements were generally restricted to within 25 m of the river channel, with the exception of one unusual piezometer more than 150 m

from the river. However, deep groundwater measurements occurred at all distances from the river (Figure 2.S2).

References

- CADWR (California Department of Water Resources) and CDFG (California Department of Fish and Game). 2003. Revegetation Plan, Merced River Salmon Habitat Enhancement Project, Robinson Reach.
- Greven, S. and T. Kneib. 2010. On the behaviour of marginal and conditional AIC in linear mixed models. *Biometrika* **97**: 773–789.
- Vaida, F. and S. Blanchard. 2005. Conditional Akaike information for mixed-effects models. *Biometrika* **92**: 351–370.

Supporting Tables

Table 2.S1. The number of transects grouped by the treatment combination applied.

Component treatments were a sterile barley cover crop (BAR), sowing select native species (SEED), and inoculating with mycorrhizae (MYCO). The three transects from the unrestored area are not included.

BAR	SEED	MYCO	Transects
No	No	No	20
Yes	No	No	26
Yes	Yes	No	6
No	Yes	Yes	4
Yes	Yes	Yes	12

Table 2.S2. All observed species grouped by NMDS cluster, sorted by mean percent cover.

NMDS Group	Species	Mean Cover (%)
unrestored	<i>Bromus diandrus</i>	10.3
unrestored	<i>Lupinus</i> spp.	4.0
unrestored	<i>Bromus hordeaceus</i>	3.2
unrestored	<i>Hypochaeris glabra</i>	2.9
unrestored	<i>Erodium</i> spp.	2.6
unrestored	<i>Avena</i> spp.	2.0
unrestored	<i>Eschscholzia californica</i>	1.8
unrestored	<i>Cucurbita palmata</i>	1.6
unrestored	<i>Croton setigerus</i>	1.5
unrestored	<i>Festuca octoflora</i>	1.1
unrestored	<i>Festuca microstachys</i>	0.9
unrestored	<i>Medicago polymorpha</i>	0.9
unrestored	<i>Trifolium</i> spp.	0.8
unrestored	<i>Bromus madritensis</i> ssp. <i>rubens</i>	0.8
unrestored	<i>Festuca myuros</i>	0.4
unrestored	<i>Acmispon americanus</i> var. <i>americanus</i>	0.4
unrestored	<i>Crassula connata</i>	0.2
unrestored	<i>Schismus arabicus</i>	0.2
unrestored	<i>Vicia sativa</i>	0.2
unrestored	<i>Logfia gallica</i>	0.1
unrestored	<i>Plantago erecta</i>	0.1
unrestored	<i>Calandrinia ciliata</i>	0.1
unrestored	<i>Heterotheca grandiflora</i>	0.1
unrestored	<i>Lepidium campestre</i>	0.1
unrestored	<i>Brassica nigra</i>	0.1
unrestored	<i>Centaurea solstitialis</i>	0.1
unrestored	<i>Cerastium glomeratum</i>	<0.05
unrestored	<i>Epilobium brachycarpum</i>	<0.05
unrestored	<i>Silene gallica</i>	<0.05
unrestored	unknown spp.	2.9
zone 4	<i>Cynodon dactylon</i>	11.8
zone 4	<i>Melilotus albus</i>	8.1
zone 4	<i>Cyperus</i> spp.	7.8
zone 4	<i>Echinochloa crus-galli</i>	6.6
zone 4	<i>Acmispon americanus</i> var. <i>americanus</i>	5.5
zone 4	<i>Eleocharis</i> spp.	3.0
zone 4	<i>Paspalum dilatatum</i>	2.5
zone 4	<i>Sorghum halepense</i>	2.1
zone 4	<i>Persicaria hydropiperoides</i>	2.1
zone 4	<i>Juncus</i> spp.	1.9

NMDS Group	Species	Mean Cover (%)
zone 4	<i>Artemisia douglasiana</i>	1.7
zone 4	<i>Pseudognaphalium luteoalbum</i>	1.6
zone 4	<i>Polypogon monspeliensis</i>	1.4
zone 4	<i>Marsilea vestita</i> ssp. <i>vestita</i>	1.3
zone 4	<i>Symphyotrichum subulatum</i>	1.0
zone 4	<i>Elymus triticoides</i>	1.0
zone 4	<i>Zeltnera venusta</i>	0.9
zone 4	<i>Typha angustifolia</i>	0.8
zone 4	<i>Digitaria sanguinalis</i>	0.8
zone 4	<i>Spergularia bocconi</i>	0.8
zone 4	<i>Festuca microstachys</i>	0.7
zone 4	<i>Verbena bonariensis</i>	0.7
zone 4	<i>Ludwigia peploides</i> ssp. <i>peploides</i>	0.6
zone 4	<i>Brassica nigra</i>	0.6
zone 4	<i>Setaria viridis</i>	0.5
zone 4	<i>Centaurea solstitialis</i>	0.5
zone 4	<i>Hordeum vulgare</i>	0.5
zone 4	<i>Leersia oryzoides</i>	0.5
zone 4	<i>Xanthium strumarium</i>	0.5
zone 4	<i>Erigeron canadensis</i>	0.4
zone 4	<i>Agrostis gigantea</i>	0.4
zone 4	<i>Polygonum aviculare</i> ssp. <i>depressum</i>	0.4
zone 4	<i>Lythrum hyssopifolium</i>	0.3
zone 4	<i>Persicaria lapathifolia</i>	0.3
zone 4	<i>Lactuca serriola</i>	0.3
zone 4	<i>Chenopodium album</i>	0.3
zone 4	<i>Epilobium ciliatum</i>	0.2
zone 4	<i>Ammannia robusta</i>	0.2
zone 4	<i>Epilobium brachycarpum</i>	0.2
zone 4	<i>Erigeron bonariensis</i>	0.2
zone 4	<i>Distichlis spicata</i>	0.1
zone 4	<i>Deschampsia danthonioides</i>	0.1
zone 4	<i>Rumex crispus</i>	0.1
zone 4	<i>Panicum dichotomiflorum</i>	0.1
zone 4	<i>Rotala ramosior</i>	0.1
zone 4	<i>Zeltnera muehlenbergii</i>	0.1
zone 4	<i>Croton setigerus</i>	0.1
zone 4	<i>Leptochloa fusca</i> ssp. <i>fascicularis</i>	0.1
zone 4	<i>Melilotus indicus</i>	0.1
zone 4	<i>Mimulus guttatus</i>	0.1
zone 4	<i>Helianthus annuus</i>	0.1
zone 4	<i>Trifolium</i> spp.	0.1

NMDS Group	Species	Mean Cover (%)
zone 4	<i>Festuca perennis</i>	0.1
zone 4	<i>Sonchus oleraceus</i>	0.1
zone 4	<i>Carex</i> spp.	0.1
zone 4	<i>Sonchus asper</i>	0.1
zone 4	<i>Veronica anagallis-aquatica</i>	<0.05
zone 4	<i>Festuca myuros</i>	<0.05
zone 4	<i>Achillea millefolium</i>	<0.05
zone 4	<i>Logfia gallica</i>	<0.05
zone 4	<i>Hypochaeris glabra</i>	<0.05
zone 4	<i>Helminthotheca echioides</i>	<0.05
zone 4	<i>Chamaesyce maculata</i>	<0.05
zone 4	<i>Veronica peregrina</i> ssp. <i>xalapensis</i>	<0.05
zone 4	<i>Epilobium densiflorum</i>	<0.05
zone 4	<i>Erodium</i> spp.	<0.05
zone 4	<i>Hordeum marinum</i>	<0.05
zone 4	<i>Hypericum anagalloides</i>	<0.05
zone 4	<i>Solanum nigrum</i>	<0.05
zone 4	<i>Dysphania ambrosioides</i>	<0.05
zone 4	<i>Euthamia occidentalis</i>	<0.05
zone 4	<i>Panicum capillare</i>	<0.05
zone 4	<i>Anthemis cotula</i>	<0.05
zone 4	<i>Bidens laevis</i>	<0.05
zone 4	<i>Bromus hordeaceus</i>	<0.05
zone 4	<i>Lactuca saligna</i>	<0.05
zone 4	<i>Acmispon glaber</i>	<0.05
zone 4	<i>Medicago sativa</i>	<0.05
zone 4	<i>Stipa</i> spp.	<0.05
zone 4	<i>Polypogon australis</i>	<0.05
zone 4	<i>Scirpus</i> spp.	<0.05
zone 4	<i>Verbascum thapsus</i>	<0.05
zone 4	<i>Bidens frondosa</i>	<0.05
zone 4	<i>Mimulus cardinalis</i>	<0.05
zone 4	<i>Geranium molle</i>	<0.05
zone 4	<i>Myriophyllum aquaticum</i>	<0.05
zone 4	<i>Heterotheca grandiflora</i>	<0.05
zone 4	<i>Hordeum brachyantherum</i>	<0.05
zone 4	<i>Nicotiana attenuata</i>	<0.05
zone 4	<i>Vicia sativa</i>	<0.05
2002	<i>Cyperus</i> spp.	5.6
2002	<i>Echinochloa crus-galli</i>	4.2
2002	<i>Hordeum vulgare</i>	4.0
2002	<i>Persicaria hydropiperoides</i>	2.1

NMDS Group	Species	Mean Cover (%)
2002	<i>Typha angustifolia</i>	0.9
2002	<i>Chenopodium album</i>	0.7
2002	<i>Eleocharis</i> spp.	0.7
2002	<i>Croton setigerus</i>	0.5
2002	<i>Acmispon americanus</i> var. <i>americanus</i>	0.5
2002	<i>Brassica nigra</i>	0.5
2002	<i>Agrostis gigantea</i>	0.4
2002	<i>Kickxia elatine</i>	0.4
2002	<i>Cynodon dactylon</i>	0.3
2002	<i>Ammannia robusta</i>	0.3
2002	<i>Ludwigia peploides</i> ssp. <i>peploides</i>	0.3
2002	<i>Pseudognaphalium luteoalbum</i>	0.3
2002	<i>Lythrum hyssopifolium</i>	0.2
2002	<i>Melilotus albus</i>	0.2
2002	<i>Polypogon monspeliensis</i>	0.2
2002	<i>Leptochloa fusca</i> ssp. <i>fascicularis</i>	0.2
2002	<i>Erigeron canadensis</i>	0.1
2002	<i>Centaurea solstitialis</i>	0.1
2002	<i>Spergularia bocconi</i>	0.1
2002	<i>Sorghum halepense</i>	0.1
2002	<i>Xanthium strumarium</i>	0.1
2002	<i>Setaria viridis</i>	0.1
2002	<i>Digitaria sanguinalis</i>	0.1
2002	<i>Veronica anagallis-aquatica</i>	0.1
2002	<i>Rotala ramosior</i>	<0.05
2002	<i>Juncus</i> spp.	<0.05
2002	<i>Panicum capillare</i>	<0.05
2002	<i>Veronica peregrina</i> ssp. <i>xalapensis</i>	<0.05
2002	<i>Verbena bonariensis</i>	<0.05
2002	<i>Erodium</i> spp.	<0.05
2002	<i>Anagallis arvensis</i>	<0.05
2002	<i>Dysphania ambrosioides</i>	<0.05
2002	<i>Solanum nigrum</i>	<0.05
2002	<i>Heterotheca grandiflora</i>	<0.05
2002	<i>Zeltnera venusta</i>	<0.05
2002	<i>Trifolium</i> spp.	<0.05
2002	<i>Helianthus annuus</i>	<0.05
2002	<i>Verbena hastata</i>	<0.05
2002	<i>Grindelia camporum</i>	<0.05
2002	<i>Leersia oryzoides</i>	<0.05
2002	<i>Paspalum dilatatum</i>	<0.05
2002	<i>Scirpus</i> spp.	<0.05

NMDS Group	Species	Mean Cover (%)
2002	<i>Sonchus oleraceus</i>	<0.05
2002	<i>Polygonum aviculare</i> ssp. <i>depressum</i>	<0.05
2002	<i>Nicotiana attenuata</i>	<0.05
2002	<i>Crypsis schoenoides</i>	<0.05
2002	<i>Anthemis cotula</i>	<0.05
2002	<i>Herniaria hirsuta</i>	<0.05
2002	<i>Lupinus</i> spp.	<0.05
2002	<i>Rorippa palustris</i>	<0.05
2002	<i>Vicia sativa</i>	<0.05
2002	<i>Marrubium vulgare</i>	<0.05
2002	unknown spp.	<0.05
SEED transient	<i>Festuca microstachys</i>	14.9
SEED transient	<i>Acmispon americanus</i> var. <i>americanus</i>	9.2
SEED transient	<i>Hordeum vulgare</i>	7.0
SEED transient	<i>Brassica nigra</i>	5.7
SEED transient	<i>Lupinus</i> spp.	4.5
SEED transient	<i>Melilotus albus</i>	2.1
SEED transient	<i>Vicia sativa</i>	1.5
SEED transient	<i>Centaurea solstitialis</i>	1.1
SEED transient	<i>Erodium</i> spp.	1.0
SEED transient	<i>Artemisia douglasiana</i>	0.8
SEED transient	<i>Trifolium</i> spp.	0.7
SEED transient	<i>Medicago polymorpha</i>	0.5
SEED transient	<i>Spergularia bocconi</i>	0.5
SEED transient	<i>Bromus diandrus</i>	0.4
SEED transient	<i>Silene gallica</i>	0.2
SEED transient	<i>Chenopodium album</i>	0.2
SEED transient	<i>Polypogon monspeliensis</i>	0.2
SEED transient	<i>Juncus</i> spp.	0.2
SEED transient	<i>Achillea millefolium</i>	0.2
SEED transient	<i>Festuca perennis</i>	0.2
SEED transient	<i>Hypochaeris glabra</i>	0.2
SEED transient	<i>Epilobium brachycarpum</i>	0.1
SEED transient	<i>Stipa</i> spp.	0.1
SEED transient	<i>Festuca myuros</i>	0.1
SEED transient	<i>Calandrinia ciliata</i>	0.1
SEED transient	<i>Logfia gallica</i>	0.1
SEED transient	<i>Croton setigerus</i>	0.1
SEED transient	<i>Polygonum aviculare</i> ssp. <i>depressum</i>	0.1
SEED transient	<i>Rumex crispus</i>	0.1
SEED transient	<i>Amsinckia menziesii</i>	<0.05
SEED transient	<i>Anthemis cotula</i>	<0.05

NMDS Group	Species	Mean Cover (%)
SEED transient	<i>Acmispon strigosus</i>	<0.05
SEED transient	<i>Spergula arvensis</i>	<0.05
SEED transient	<i>Lactuca serriola</i>	<0.05
SEED transient	<i>Pseudognaphalium luteoalbum</i>	<0.05
SEED transient	<i>Hordeum brachyantherum</i>	<0.05
SEED transient	<i>Cryptogramma</i> spp.	<0.05
SEED transient	<i>Erigeron canadensis</i>	<0.05
SEED transient	<i>Lythrum hyssopifolium</i>	<0.05
SEED transient	<i>Heterotheca grandiflora</i>	<0.05
SEED transient	<i>Bromus hordeaceus</i>	<0.05
SEED transient	<i>Cyperus</i> spp.	<0.05
SEED transient	<i>Herniaria hirsuta</i>	<0.05
SEED transient	<i>Anagallis arvensis</i>	<0.05
SEED transient	<i>Nicotiana attenuata</i>	<0.05
SEED transient	<i>Persicaria hydropiperoides</i>	<0.05
SEED transient	<i>Sonchus oleraceus</i>	<0.05
SEED transient	<i>Stellaria media</i>	<0.05
SEED transient	<i>Verbena bonariensis</i>	<0.05
SEED transient	<i>Xanthium strumarium</i>	<0.05
SEED transient	<i>Veronica peregrina</i> ssp. <i>xalapensis</i>	<0.05
SEED transient	<i>Briza minor</i>	<0.05
SEED transient	<i>Chorizanthe membranacea</i>	<0.05
SEED transient	<i>Crassula connata</i>	<0.05
SEED transient	<i>Echinochloa crus-galli</i>	<0.05
SEED transient	<i>Lactuca saligna</i>	<0.05
SEED transient	<i>Elymus triticoides</i>	<0.05
SEED transient	<i>Melica californica</i>	<0.05
flood	<i>Polypogon monspeliensis</i>	2.7
flood	<i>Lythrum hyssopifolium</i>	1.7
flood	<i>Polygonum aviculare</i> ssp. <i>depressum</i>	1.6
flood	<i>Cynodon dactylon</i>	1.5
flood	<i>Brassica nigra</i>	1.3
flood	<i>Festuca perennis</i>	1.1
flood	<i>Chamaesyce maculata</i>	1.1
flood	<i>Xanthium strumarium</i>	1.1
flood	<i>Spergularia bocconi</i>	0.8
flood	<i>Centaurea solstitialis</i>	0.7
flood	<i>Echinochloa crus-galli</i>	0.6
flood	<i>Acemispon americanus</i> var. <i>americanus</i>	0.6
flood	<i>Phyla nodiflora</i>	0.6
flood	<i>Cyperus</i> spp.	0.5
flood	<i>Persicaria hydropiperoides</i>	0.5

NMDS Group	Species	Mean Cover (%)
flood	<i>Lactuca saligna</i>	0.5
flood	<i>Poa annua</i>	0.5
flood	<i>Croton setigerus</i>	0.5
flood	<i>Crypsis schoenoides</i>	0.4
flood	<i>Digitaria sanguinalis</i>	0.4
flood	<i>Artemisia douglasiana</i>	0.4
flood	<i>Erodium</i> spp.	0.4
flood	<i>Setaria viridis</i>	0.3
flood	<i>Hypochaeris glabra</i>	0.3
flood	<i>Symphyotrichum subulatum</i>	0.3
flood	<i>Amaranthus albus</i>	0.3
flood	<i>Persicaria lapathifolia</i>	0.3
flood	<i>Bidens frondosa</i>	0.2
flood	<i>Epilobium brachycarpum</i>	0.2
flood	<i>Rumex crispus</i>	0.2
flood	<i>Chenopodium album</i>	0.2
flood	<i>Elymus triticoides</i>	0.2
flood	<i>Trifolium</i> spp.	0.2
flood	<i>Sorghum halepense</i>	0.2
flood	<i>Melilotus albus</i>	0.2
flood	<i>Festuca myuros</i>	0.1
flood	<i>Bromus hordeaceus</i>	0.1
flood	<i>Sonchus oleraceus</i>	0.1
flood	<i>Grindelia camporum</i>	0.1
flood	<i>Erigeron canadensis</i>	0.1
flood	<i>Anthemis cotula</i>	0.1
flood	<i>Kickxia elatine</i>	0.1
flood	<i>Juncus</i> spp.	0.1
flood	<i>Leersia oryzoides</i>	<0.05
flood	<i>Eleocharis</i> spp.	<0.05
flood	<i>Helianthus annuus</i>	<0.05
flood	<i>Stipa</i> spp.	<0.05
flood	<i>Vicia sativa</i>	<0.05
flood	<i>Spergula arvensis</i>	<0.05
flood	<i>Pseudognaphalium luteoalbum</i>	<0.05
flood	<i>Myriophyllum aquaticum</i>	<0.05
flood	<i>Typha angustifolia</i>	<0.05
flood	<i>Anagallis arvensis</i>	<0.05
flood	<i>Bromus diandrus</i>	<0.05
flood	<i>Panicum dichotomiflorum</i>	<0.05
flood	<i>Nicotiana attenuata</i>	<0.05
flood	<i>Medicago polymorpha</i>	<0.05

NMDS Group	Species	Mean Cover (%)
flood	<i>Solanum nigrum</i>	<0.05
flood	<i>Cucurbita palmata</i>	<0.05
flood	<i>Rubus armeniacus</i>	<0.05
flood	<i>Alternanthera caracasana</i>	<0.05
flood	<i>Portulaca oleracea</i>	<0.05
flood	<i>Veronica peregrina</i> ssp. <i>xalapensis</i>	<0.05
flood	<i>Herniaria hirsuta</i>	<0.05
flood	<i>Helminthotheca echioides</i>	<0.05
flood	<i>Dysphania ambrosioides</i>	<0.05
flood	<i>Ludwigia peploides</i> ssp. <i>peploides</i>	<0.05
flood	<i>Zeltnera muehlenbergii</i>	<0.05
flood	<i>Hordeum vulgare</i>	<0.05
flood	<i>Lupinus</i> spp.	<0.05
flood	<i>Logfia gallica</i>	<0.05
flood	<i>Achillea millefolium</i>	<0.05
flood	<i>Deschampsia danthonioides</i>	<0.05
flood	<i>Lactuca serriola</i>	<0.05
flood	<i>Silene gallica</i>	<0.05
flood	<i>Eschscholzia californica</i>	<0.05
flood	<i>Urtica dioica</i> ssp. <i>gracilis</i>	<0.05
flood	<i>Festuca microstachys</i>	<0.05
flood	unknown spp.	0.9
non-flood	<i>Erodium</i> spp.	6.6
non-flood	<i>Acmispon americanus</i> var. <i>americanus</i>	6.4
non-flood	<i>Trifolium</i> spp.	3.8
non-flood	<i>Brassica nigra</i>	3.0
non-flood	<i>Spergularia bocconi</i>	2.5
non-flood	<i>Lupinus</i> spp.	2.4
non-flood	<i>Melilotus albus</i>	2.2
non-flood	<i>Festuca myuros</i>	1.8
non-flood	<i>Polypogon monspeliensis</i>	1.8
non-flood	<i>Festuca microstachys</i>	1.4
non-flood	<i>Cryptogramma</i> spp.	1.3
non-flood	<i>Hypochaeris glabra</i>	1.1
non-flood	<i>Hordeum vulgare</i>	1.0
non-flood	<i>Logfia gallica</i>	0.7
non-flood	<i>Silene gallica</i>	0.7
non-flood	<i>Bromus diandrus</i>	0.6
non-flood	<i>Medicago polymorpha</i>	0.6
non-flood	<i>Festuca perennis</i>	0.4
non-flood	<i>Crassula connata</i>	0.4
non-flood	<i>Calandrinia ciliata</i>	0.4

NMDS Group	Species	Mean Cover (%)
non-flood	<i>Bromus hordeaceus</i>	0.3
non-flood	<i>Juncus</i> spp.	0.3
non-flood	<i>Vicia sativa</i>	0.3
non-flood	<i>Artemisia douglasiana</i>	0.3
non-flood	<i>Centaurea solstitialis</i>	0.2
non-flood	<i>Spergula arvensis</i>	0.2
non-flood	<i>Epilobium brachycarpum</i>	0.2
non-flood	<i>Anthemis cotula</i>	0.2
non-flood	<i>Erigeron canadensis</i>	0.2
non-flood	<i>Cucurbita palmata</i>	0.2
non-flood	<i>Anagallis arvensis</i>	0.2
non-flood	<i>Marrubium vulgare</i>	0.2
non-flood	<i>Poa annua</i>	0.2
non-flood	<i>Cerastium glomeratum</i>	0.2
non-flood	<i>Lythrum hyssopifolium</i>	0.1
non-flood	<i>Festuca octoflora</i>	0.1
non-flood	<i>Sonchus oleraceus</i>	0.1
non-flood	<i>Schismus arabicus</i>	0.1
non-flood	<i>Bromus madritensis</i> ssp. <i>rubens</i>	0.1
non-flood	<i>Croton setigerus</i>	0.1
non-flood	<i>Eschscholzia californica</i>	0.1
non-flood	<i>Polygonum aviculare</i> ssp. <i>depressum</i>	0.1
non-flood	<i>Pseudognaphalium luteoalbum</i>	0.1
non-flood	<i>Avena</i> spp.	0.1
non-flood	<i>Callitriche marginata</i>	<0.05
non-flood	<i>Setaria viridis</i>	<0.05
non-flood	<i>Senecio vulgaris</i>	<0.05
non-flood	<i>Lactuca serriola</i>	<0.05
non-flood	<i>Grindelia camporum</i>	<0.05
non-flood	<i>Persicaria hydropiperoides</i>	<0.05
non-flood	<i>Acmispon strigosus</i>	<0.05
non-flood	<i>Datura wrightii</i>	<0.05
non-flood	<i>Veronica peregrina</i> ssp. <i>xalapensis</i>	<0.05
non-flood	<i>Amsinckia menziesii</i>	<0.05
non-flood	<i>Cynodon dactylon</i>	<0.05
non-flood	<i>Elymus triticoides</i>	<0.05
non-flood	<i>Stellaria media</i>	<0.05
non-flood	<i>Cyperus</i> spp.	<0.05
non-flood	<i>Epilobium ciliatum</i>	<0.05
non-flood	<i>Hordeum murinum</i>	<0.05
non-flood	<i>Matricaria discoidea</i>	<0.05
non-flood	<i>Rumex crispus</i>	<0.05

NMDS Group	Species	Mean Cover (%)
non-flood	<i>Lepidium campestre</i>	<0.05
non-flood	<i>Chenopodium album</i>	<0.05
non-flood	<i>Herniaria hirsuta</i>	<0.05
non-flood	<i>Heterotheca grandiflora</i>	<0.05
non-flood	<i>Plantago erecta</i>	<0.05
non-flood	<i>Aira caryophyllea</i>	<0.05
non-flood	<i>Dysphania ambrosioides</i>	<0.05
non-flood	<i>Cirsium vulgare</i>	<0.05
non-flood	<i>Distichlis spicata</i>	<0.05
non-flood	<i>Galium aparine</i>	<0.05
non-flood	<i>Medicago lupulina</i>	<0.05
non-flood	<i>Stipa</i> spp.	<0.05
non-flood	<i>Helminthotheca echioides</i>	<0.05
non-flood	<i>Rumex acetosella</i>	<0.05
non-flood	<i>Sonchus arvensis</i>	<0.05
non-flood	<i>Verbena bonariensis</i>	<0.05
non-flood	<i>Achillea millefolium</i>	<0.05
non-flood	<i>Chamaesyce maculata</i>	<0.05
non-flood	<i>Melica californica</i>	<0.05
non-flood	unknown spp.	0.2

Table 2.S3. The number of transects surveyed in each year grouped by zone and treatments applied.

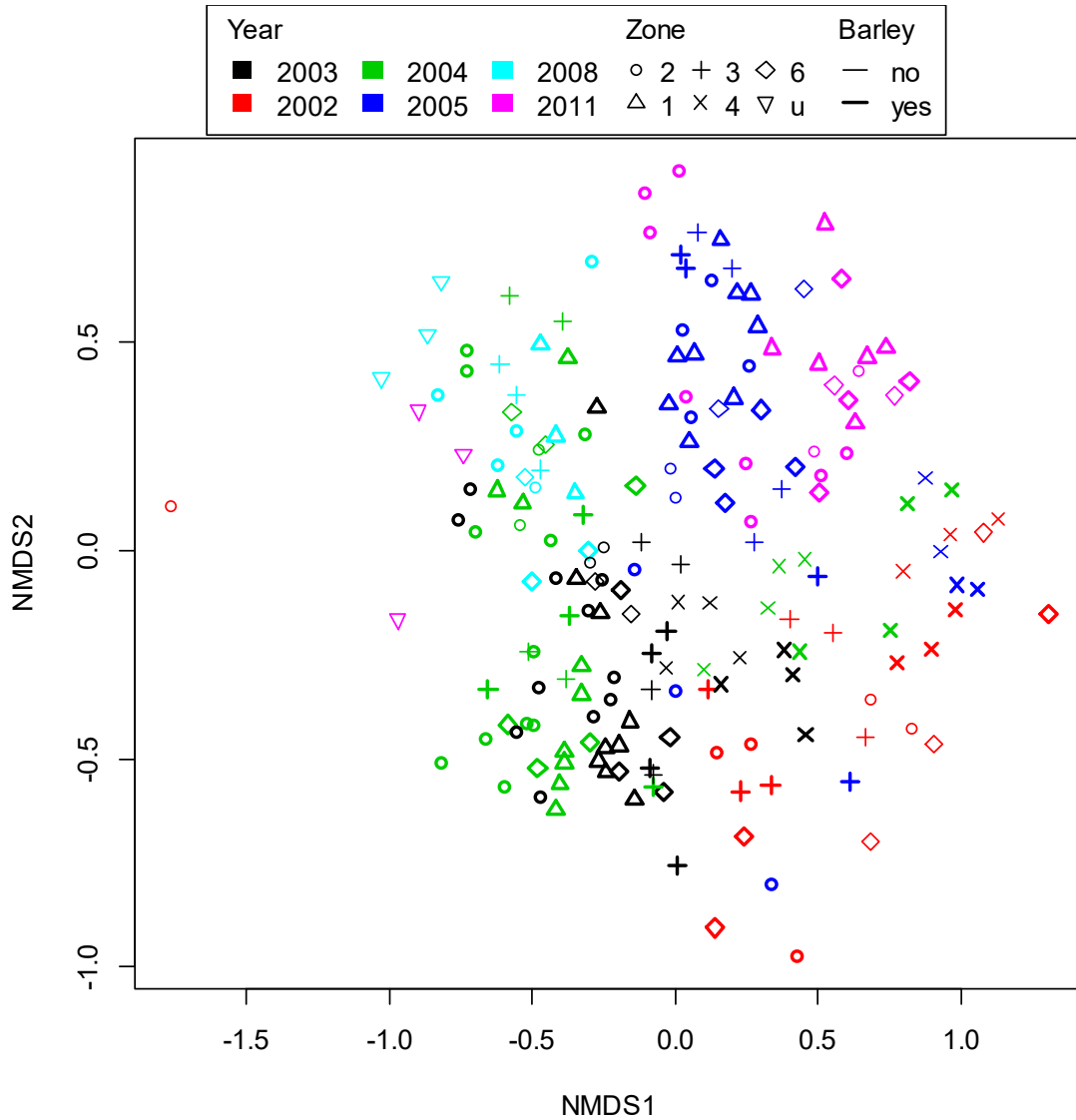
Zone	Barley	Seeded	Mycorrhizae	2002	2003	2004	2005	2008	2011
1	Yes	No	No	0	3	3	3	1	2
1	Yes	Yes	No	0	3	3	3	1	2
1	Yes	Yes	Yes	0	3	3	3	1	2
2	No	No	No	3	2	2	2	1	2
2	Yes	No	No	3	5	5	4	2	4
2	Yes	Yes	No	0	3	3	0	1	2
2	Yes	Yes	Yes	0	3	3	0	1	2
3	No	No	No	3	2	2	2	2	0
3	No	Yes	Yes	0	2	2	2	1	0
3	Yes	No	No	3	2	2	2	0	0
3	Yes	Yes	Yes	0	2	2	2	0	0
4	No	No	No	3	2	2	0	0	0
4	No	Yes	Yes	0	2	2	2	0	0
4	Yes	No	No	3	2	2	0	0	0
4	Yes	Yes	Yes	0	2	2	2	0	0
6	No	No	No	3	2	2	2	1	2
6	Yes	No	No	3	2	2	2	1	2
6	Yes	Yes	Yes	0	2	2	2	1	2
Unrestored	No	No	No	0	0	0	0	3	3

Table 2.S4. Model fit as a function of the scale of included spatial random effects. Models included all main fixed and random effects indicated in Table 2.2, except for the spatial random effects, which were as indicated here.

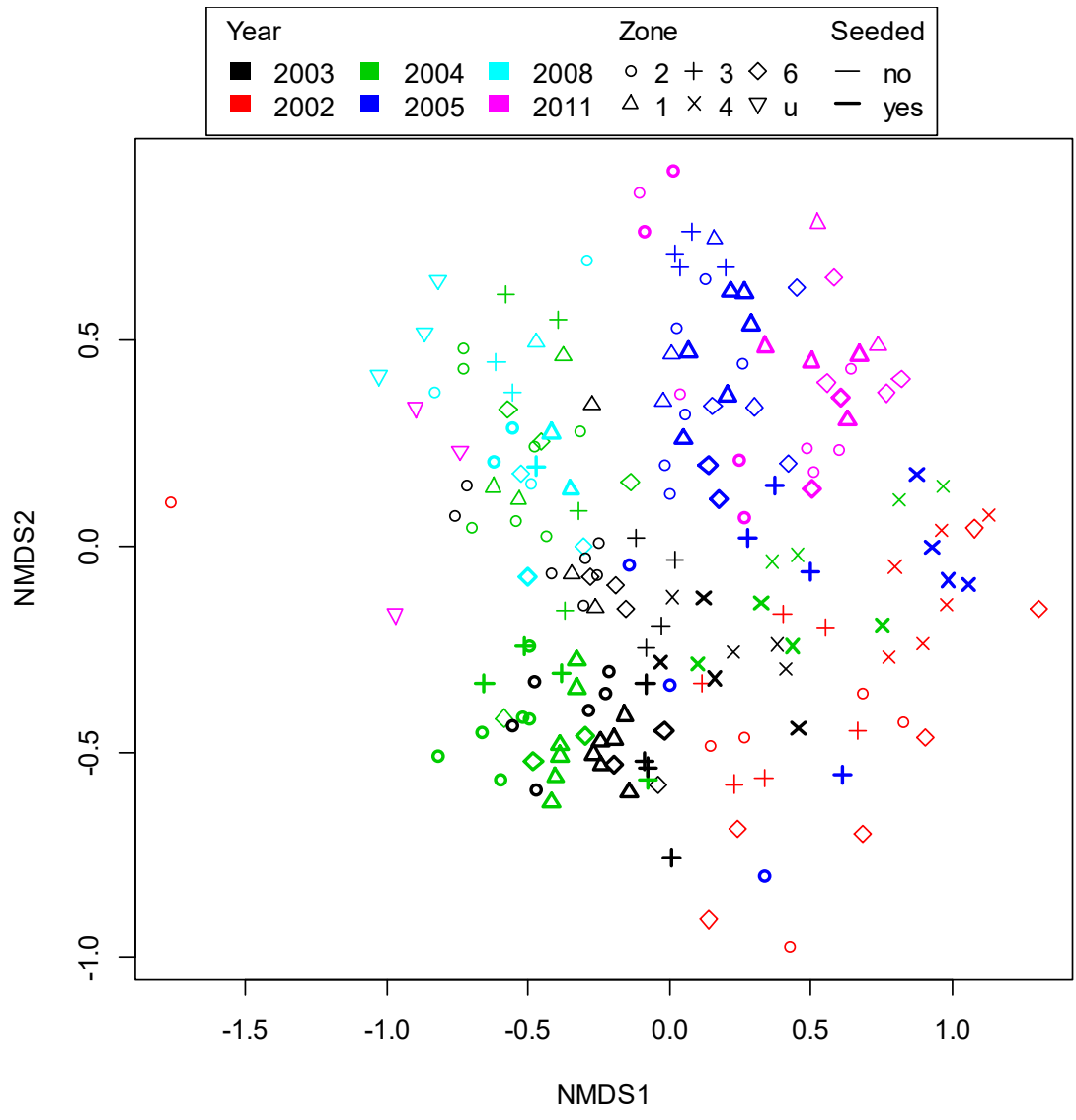
Model	log(\mathcal{L})	d.f.	mAIC	ΔmAIC
Response: total cover (%)				
Zone	-8,252.62	23	16,551.23	149.57
Zone, transect	-8,176.83	24	16,401.66	0.00
Zone, transect, plot	-8,176.03	25	16,402.06	0.40
Response: richness (S)				
Zone	-3,778.78	23	7,603.57	108.22
Zone, transect	-3,723.67	24	7,495.35	0.00
Zone, transect, plot	-3,723.67	25	7,497.35	2.00
Response: diversity (H)				
Zone	-1,149.02	23	2,344.03	64.58
Zone, transect	-1,115.73	24	2,279.46	0.00
Zone, transect, plot	-1,115.73	25	2,281.46	2.00

Supporting Figures

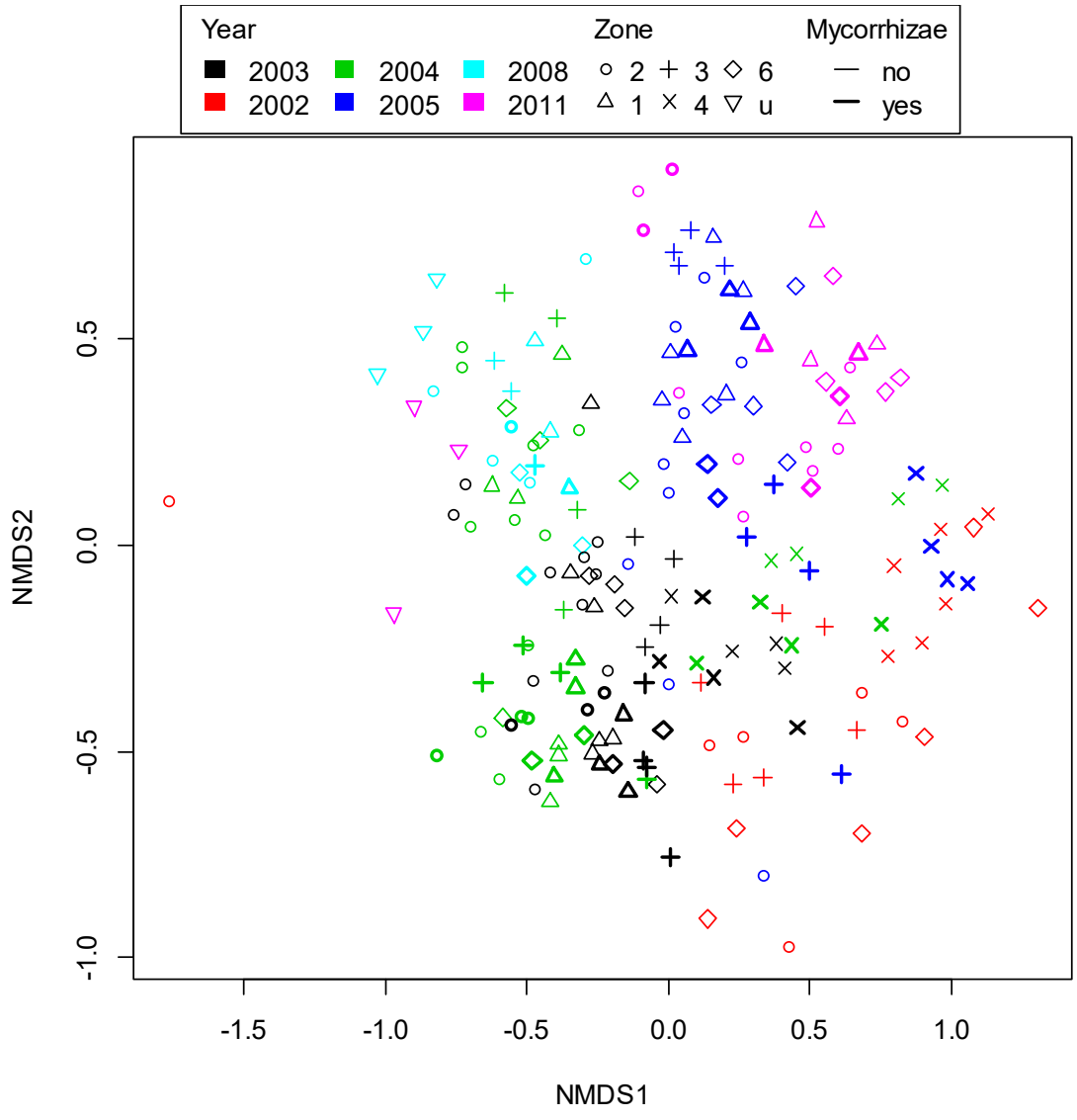
Figure 2.S1. Observations of survey transects in NMDS ordination space indicating the survey year, management zone, and whether a transect was a) sown with barley, b) seeded with native species, or c) inoculated with mycorrhizae. Zone u identifies transects in the unrestored reach.



a)

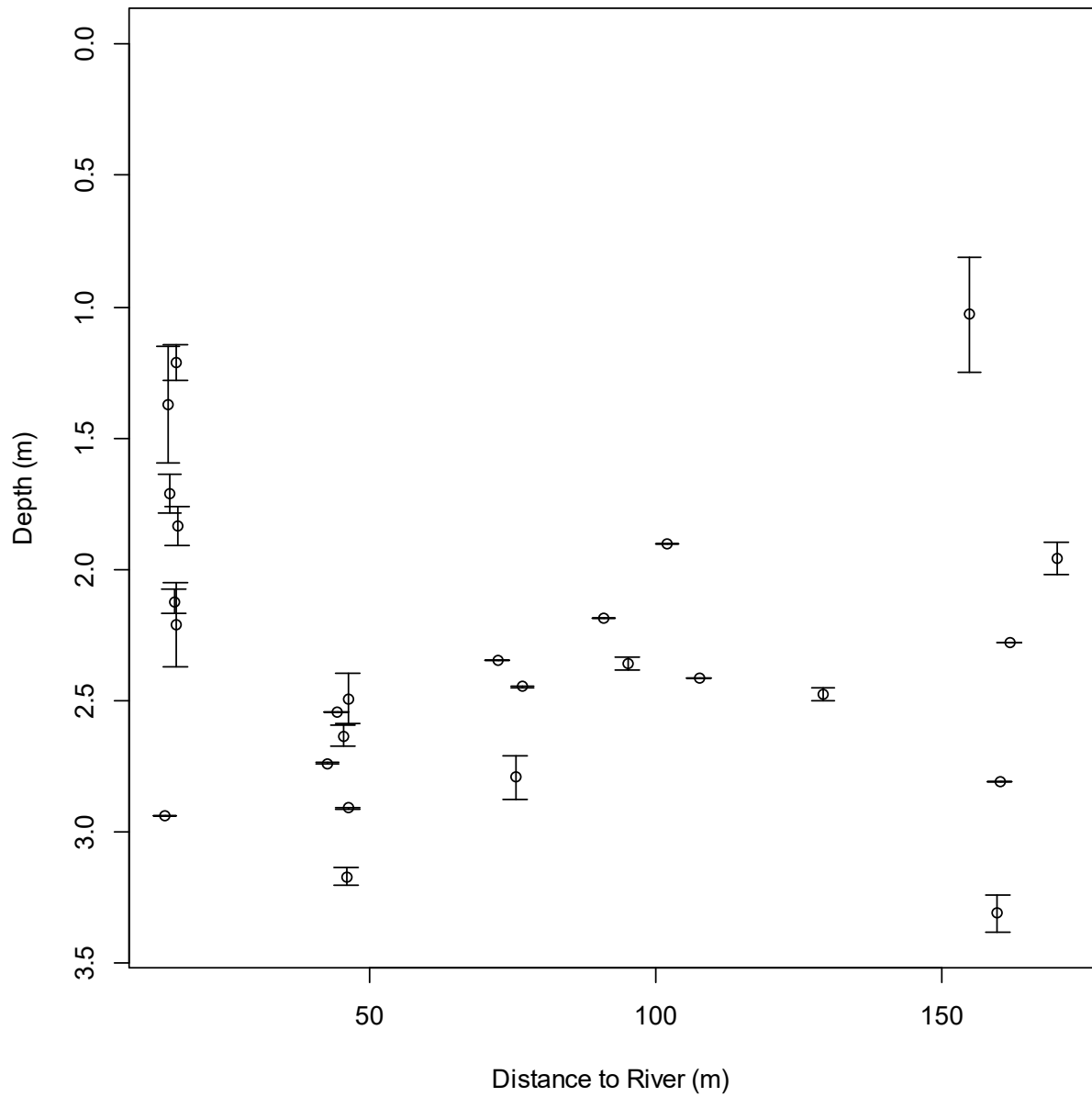


b)



c)

Figure 2.S2. Depth to groundwater during 2010 in relation to the distance of the piezometer from the river. Points and error bars represent the mean \pm 1 standard error.



3. Efficient Estimation of Capture-recapture Data: A Generalized Multistate and Multievent Model of Poisson Recruitment

Introduction

Wildlife and wildlands management is facilitated by improvements in our understanding of and capabilities to estimate and predict recruitment and survivorship rates of component populations. However, surveys to estimate such demographic rates are often obscured by uncertainty in the observation process itself. For example, riparian management and restoration efforts would benefit from an improved understanding of where species are capable of natural establishment, but seedlings are small and easily overlooked. Such false absences are common, both for animal capture-recapture studies, in which recovery rates can be quite low, and for plant studies (Chen et al., 2009). Certain plants, including many riparian trees, are especially troublesome, as they maintain persistent and unobserved belowground structures that can produce new growth even when the aboveground structures that are typically surveyed are missing, perhaps due to having been grazed or gone dormant.

Various derivatives of the venerable Jolly-Seber (JS) model of capture-recapture data (Jolly, 1965; Seber, 1965) have been developed to estimate demographic rates and their relationships to environmental covariates, even in the presence of false absences, and such capture-recapture models have been used in diverse contexts ranging from whales (Fujiwara and Caswell, 2002), birds (Pradel, 2005), mammals (Nichols et al., 1992), and even plants (Alexander, Slade, and Kettle, 1997; Shefferson et al., 2001). These capture-recapture models have been gradually improved and generalized to apply to progressively more realistic population models and complex observations. Three advances are particularly interesting: the generalization of the population process for multiple survey locations and

stage-structured populations (Arnason, 1972; Nichols et al., 1992), the generalization of the observation process for imperfect state assessments (Pradel, 2005), and an internally consistent treatment of recruitment (Pradel, 1996; Schwarz and Arnason, 1996). Although the generalized population and observation processes have been combined within hidden Markov models (HMM; Pradel, 2005; Gimenez et al., 2012), and although a generalized population process has been combined with an internally consistent treatment of recruitment (Dupuis and Schwarz, 2007), we are not aware of any models combining all three elements.

The generalization of the population process has broadened the range of populations that can be modeled. The original JS model can be applied to a heterogeneous population, such as one with different vital rates for the different sexes (Jolly, 1965). Migration rates between sub-populations can be modeled with a multisite model (Arnason, 1972). Transitions among life stages can be estimated in a multistate model (Nichols et al., 1992). In all of these cases, the population process can be represented as a Markov process, with the different sexes, locations, life stages, and interactions thereof treated as different states.

The generalization of the observation process has broadened the range of datasets that can be analyzed. Traditional capture-recapture models assume individual state assessments are perfectly accurate, but such assessments are frequently subjective, with potential misclassifications. For example, sexual maturity can be ambiguous when an individual is only observed foraging, and some dormant plants that appear dead will later sprout fresh new growth. On the other hand, observers can sometimes estimate their confidence in their assessments (e.g., probably immature or probably alive). Multievent models incorporate such uncertainty by fitting probability distributions for the uncertain observations conditional on the underlying state of the individual (Pradel, 2005).

Whereas survivorship has been consistently if sometimes unknowingly treated as a Markovian transition probability, capture-recapture models treat recruitment in several different ways, if at all. In the original JS models, recruitment was indirectly derived from estimated population sizes. Inconsistencies arising from this formulation led subsequent models to treat recruitment prior to the first observation analogously to survivorship after the last observation (Pradel, 1996; Schwarz and Arnason, 1996). Despite sharing a similar conceptual treatment, specific parameterizations vary from individualistic seniority rates to population fecundity rates (Pradel, 1996) to superpopulation entry probabilities (Schwarz and Arnason, 1996). In certain special cases, recruitment can be defined as a life history transition, such as accession to reproduction, and can be estimated through a multistate model (Lebreton and Pradel, 2002).

Despite this progress, approaches to recruitment in capture-recapture models are still limited. There are many cases where recruitment cannot be easily defined as a life history transition, such as when estimating the recruitment rate of truly new and hence unmarked individuals. Additionally, even though seniority rates, fecundity rates, and superpopulation entry probabilities are mathematically proper, they can be unintuitive, inconvenient, and sometimes uninterpretable. For example, recruitment studies are sometimes restricted to non-reproductive juveniles, for whom traditional fecundity estimates are the nonsensical number of juveniles born per non-reproductive juvenile. Similar difficulties are encountered when the underlying population model includes a non-reproductive class. Furthermore, the superpopulation of individuals ever available for capture is an inherently study-specific parameter, as are the associated probabilities of entry into the population of individuals currently available for capture, and are not utilized by any population model. Although

recruitment can be naturally expressed as an inhomogeneous Poisson process, such processes have rarely been incorporated in capture-recapture models (e.g., O’Hara et al., 2009).

Although all of these models have been useful, there are situations in which each is only partially applicable, such as estimating the recruitment rate of seedlings at several sites of differing quality when aboveground appearance is an imperfect indication of individual condition. We first describe a generic system with discrete states, observations, and survey occasions, and then describe a hidden process model based upon Poisson recruitment that incorporates multistate and multievent models and is closely related to superpopulation entry probability models but parameterized in a more intuitive and ecologically relevant manner. We then briefly write the hidden Markov model used by most extant capture-recapture models. Finally, we use example applications to simulated and real datasets of *Salix gooddingii* seedlings to demonstrate how to model the relationship between environmental covariates and demographic rates as well as conditions that influence the precision of parameter estimates.

Hidden Process Model

We present a generic hidden process model with discrete states, observations, and survey occasions that can be used to describe many population demographic studies. Let $\boldsymbol{\tau}' = \{\tau'_i\}$ be the set of states an individual might exist in at a particular time, where an individual state can be physiological (e.g., sexually mature, of harvestable size, or 3 years old), spatial (e.g., site A), or some combination of these. For convenience, we include the unborn and dead states in $\boldsymbol{\tau}'$. During the study period, individuals may transition within $\boldsymbol{\tau}'$, and the sequence of states defines the “fate” of the individual over the study period. Let $\boldsymbol{\tau} = \{\tau_i\}$ be the set of

possible fates an individual might experience. For example, an individual might have not yet recruited (τ'_0), might be alive at some site $\rho \in \boldsymbol{\rho}$ ($\tau'_{1,\rho}$), or might be dead at site ρ ($\tau'_{-1,\rho}$), where $\boldsymbol{\rho} = \{\rho_i\}$ is the set of all study sites. In an experiment with four surveys, the sixth fate $\tau_6 = \tau'_0 \tau'_{1,\rho_1} \tau'_{1,\rho_1} \tau'_{-1,\rho_2}$ might represent an individual that recruited between the first and second surveys, was located at site ρ_1 during the second and third surveys, and migrated to and died at site ρ_2 between the third and fourth surveys. The dynamics of this population as a whole can be completely and succinctly summarized by the vector $[n_\tau]$, where n_τ is the number of individuals that experienced fate τ .

In a hidden process model, observations are a filtered view of the actual population dynamics. Let $\boldsymbol{\psi}' = \{\psi'_i\}$ be the set of possible single observations. In a simple capture-recapture model, an individual is either detected alive (ψ'_1) or not detected (ψ'_0). In a more complicated example, an observer might declare an individual alive at site ρ ($\psi'_{1,\rho}$), probably alive at site ρ ($\psi'_{2,\rho}$), probably dead at site ρ ($\psi'_{3,\rho}$), dead at site ρ ($\psi'_{4,\rho}$), or not detected at all (ψ'_0). Let $\boldsymbol{\psi} = \{\psi_i\}$ be the set of possible ‘‘observation histories’’ (i.e., capture histories). For example, the 187th observation history $\psi_{187} = \psi'_0 \psi'_{1,\rho_1} \psi'_{3,\rho_1} \psi'_0$ might represent an individual that was not detected in the first survey, was judged alive and then probably dead at site ρ_1 in the second and third surveys, and was again not detected in the final survey. Let $\boldsymbol{\psi}^-$ be the subset of observation histories in which the individual was never detected, and let its complement $\boldsymbol{\psi}^+ = \boldsymbol{\psi} - \boldsymbol{\psi}^-$ be the subset of observation histories in which the individual was detected at some point in the study. In the example, $\boldsymbol{\psi}^-$ contains only one such history consisting solely of ψ'_0 .

To estimate the parameters of interest when the true behavior of the system is unknown, we simply treat this unknown reality as a nuisance auxiliary parameter. More specifically,

let the matrix $[n_{\tau,\psi}]$ describe one possible reality, where $n_{\tau,\psi}$ is the number of individuals that experienced fate τ and were observed with history ψ . The likelihood of each possible reality can be partitioned into recruitment, post-recruitment fates, and observations. Define cohort $c_{\tau',t}$ as the individuals that recruited in the interval between time t and $t + 1$ and existed in state τ' at time $t + 1$. For convenience, we use “recruitment” loosely when defining the $c_{\tau',0}$ cohorts, which describe the initial state of the system. All individuals that share the same fate τ belong to the same cohort $\check{c}(\tau)$, but the members of that cohort may experience any of the fates in $\boldsymbol{\tau}_c = \{\tau \mid \check{c}(\tau) = c\}$. Recruitment is often modeled as an inhomogenous Poisson process (e.g., Witt and Webster, 2010) in which n_c , the number of individuals in cohort c , is Poisson distributed with rate R_c and likelihood $\mathbb{P}(n_c|R_c)$. Let $P(\tau|c)$ be the probability that a member of cohort c experienced fate τ , and let $n_{\tau|c}$ be number of these individuals. The individuals in a cohort are therefore distributed among the fates with multinomial likelihood $\mathbb{M}([n_{\tau|c}]|[P(\tau|c)])$. Let $P(\psi|\tau)$ be the probability that an individual that experienced fate τ was observed with history ψ , and let $n_{\psi|\tau}$ be the number of these individuals. Although $n_{\tau,\psi} = n_{\psi|\tau}$, this notation distinguishes specific sub-vectors, and this convention will be used throughout. The individuals that experienced fate τ are therefore distributed among the observation histories with multinomial likelihood $\mathbb{M}([n_{\psi|\tau}]|[P(\psi|\tau)])$. The likelihood of a possible reality then comprises Poisson recruitment of cohorts, multinomial allocation of this recruitment among the possible fates, and multinomial allocation of fated individuals among the possible observation histories. For concision, we have suppressed extraneous parameters here and throughout:

$$P([n_{\tau,\psi}]) = \prod_c \mathbb{P}(n_c|R_c) \mathbb{M}([n_{\tau|c}]|[P(\tau|c)]) \prod_{\tau \in \boldsymbol{\tau}_c} \mathbb{M}([n_{\psi|\tau}]|[P(\psi|\tau)]).$$

Using simple statistical identities, we may simplify this likelihood:

$$P([n_{\tau,\psi}]) = \prod_{\tau,\psi} \mathbb{P}(n_{\tau,\psi} | R_{\tau,\psi}) = \mathbb{P}(N|R) \mathbb{M}([n_{\tau,\psi}] | [P(\tau, \psi)]),$$

where $N = \sum_{\tau,\psi} n_{\tau,\psi}$ is the standard superpopulation of all individuals ever available for capture over the duration of the study, where $R = \sum_c R_c$ is the superpopulation recruitment rate, where $P(\tau, \psi) = P(\tau) P(\psi|\tau)$ is the probability an individual experienced fate τ and was observed with history ψ , where $P(\tau) = P(\check{c}(\tau)) P(\tau | \check{c}(\tau))$ is the probability an individual experienced fate τ , where $P(c) = \beta_c = R_c/R$ is the standard superpopulation entry probability of cohort c , and where $R_{\tau,\psi} = R_{\check{c}(\tau)} P(\tau | \check{c}(\tau)) P(\psi|\tau)$ is the occurrence rate of individuals that experienced fate τ and were observed with history ψ . In particular, the β_c are equivalent to those of superpopulation entry probability models (Schwarz and Arnason, 1996; Dupuis and Schwarz, 2007), while the $R_{\tau,\psi}$ are essentially those of early Poisson capture-recapture models (Jolly, 1979).

Two approaches to parameter estimation are particularly noteworthy, the first being analytical marginalization of the $[n_{\tau,\psi}]$:

$$P([y_{\psi^+}]) = \sum_{\mathbf{c}} P([n_{\tau,\psi}]),$$

where y_{ψ^+} is the number of individuals observed with observation history ψ^+ and \mathbf{C} is the set of all possible realities consistent with the observed data:

$$\mathbf{C} = \left\{ [n_{\tau,\psi}] \left| \sum_{\tau} n_{\tau,\psi^+} = y_{\psi^+} \right. \right\}.$$

Obviously, the n_{τ,ψ^-} are unconstrained as they are by definition unobserved. Assuming the component parameters $P(\psi|\tau)$, $P(\tau|c)$, and R_c are independent of the $n_{\tau,\psi}$, the sum may be factored utilizing Cartesian products (Supporting Information):

$$P([y_{\psi^+}]|[P(\psi|\tau)], [P(\tau|c)], [R_c]) = \prod_{\psi^+} \mathbb{P}(y_{\psi^+}|R_{\psi^+}) = \mathbb{P}(y|R^+) \mathbb{M}([y_{\psi^+}]|[P^+(\psi^+)]),$$

where $y = \sum_{\psi^+} y_{\psi^+}$ is the total number of observed individuals, $R_{\psi^+} = \sum_{\tau} R_{\tau,\psi^+}$ is the total occurrence rate of individuals observed with history ψ^+ , $R^+ = \sum_{\psi^+} R_{\psi^+}$ is the total occurrence rate of observed individuals, and

$P^+(\psi^+) = R_{\psi^+}/R^+ = \sum_{\tau} P(\tau, \psi^+)/\sum_{\tau,\psi^+} P(\tau, \psi^+)$ is the truncated probability of observing an individual with history ψ^+ .

Alternatively, it is possible to directly estimate $P([n_{\tau,\psi}])$ using more advanced Bayesian data augmentation methods (e.g., Tanner and Wong, 1987; van Dyk and Meng, 2001).

Specifically, the $[n_{\tau|\psi^+}]$ form a multinomial distribution with sample size y_{ψ^+} and probabilities $[R_{\tau|\psi^+}/R_{\psi^+}]$, while the n_{τ,ψ^-} are simply Poisson distributed with rates R_{τ,ψ^-} . These Bayesian data augmentation methods are particularly useful when modeling density-dependent mortality.

In either case, we leave this model parameterized solely in terms of $P(\psi|\tau)$, $P(\tau|c)$, and R_c for the sake of generality, despite severe overparameterization. Any useful implementation would require additional case-specific constraints.

Hidden Markov Model

Although this hidden process model does not require the memoryless assumptions of an HMM, the existing capture-recapture literature does make such an assumption, and we

briefly present this specialized case for comparison. In these traditional models, the transitions of individuals among states are defined by a transition probability matrix $[\phi_{\tau'_i, \tau'_j, t}]$, where $\phi_{\tau'_i, \tau'_j, t}$ gives the probability that an individual in state τ'_i at time t is in state τ'_j at time $t + 1$. For example, the survivorship rate for individuals in state τ' from time t to time $t + 1$ is $\phi_{\tau', \tau', t}$. Let $\check{\tau}'(\tau, t)$ give the state at time t of an individual that experienced fate τ , and let $\check{\tau}(\tau)$ give the survey before an individual recruits, such that the individual is a member of some cohort $c_{\check{\tau}'(\tau, \check{\tau}(\tau)+1), \check{\tau}(\tau)}$. Let the unborn state be τ'_0 , define $\check{\tau}'(\tau, 0) = \tau'_0$, and define $\check{\tau}(\tau) = 0$ for individuals that recruited prior to the first survey. The probability of a fate τ is then a trivial product:

$$P(\tau|c) = \prod_{t > \check{\tau}(\tau)} \phi_{\check{\tau}'(\tau, t), \check{\tau}'(\tau, t+1), t}.$$

Similarly, the probability $p_{\psi'_i, \tau'_j, t}$ of observing ψ'_i at time t depends only on the state τ'_j of the individual being observed, and the $\{p_{\psi'_i, \tau'_j, t} | \tau'\}$ form a conditional distribution. Let $\check{\Psi}'(\psi, t)$ give the observation at time t of an individual with observation history ψ . The probability that an individual that experienced fate τ was observed with history ψ is similarly trivial:

$$P(\psi|\tau) = \prod_t p_{\check{\Psi}'(\psi, t), \check{\tau}'(\tau, t), t}.$$

The hidden Markov model $P\left([y_{\psi^+}] | [p_{\psi'_i, \tau'_j, t}], [\phi_{\tau'_i, \tau'_j, t}], [R_c]\right)$ has far fewer parameters than the hidden process model while retaining much useful generality, and has been sufficient in many cases, but is still prone to overparameterization.

Covariates and Hierarchical Structures

We are often interested in inferring the relationship between measured environmental covariates and demographic rates in addition to the specific rates themselves, and using hierarchical structures to model these relationships can diminish overfitting and identifiability problems in the highly generalized models presented here. In keeping with HMMs, we only consider state-specific covariates, such as site-specific measurements. For example, we might say the survivorship rate, $\phi_{\tau'_{1,\rho},\tau'_{1,\rho},t}$, varies as a function, $\phi(\vec{\theta}_\phi, \vec{x}_{\phi,\rho,t})$, of measured covariates, $\vec{x}_{\phi,\rho,t}$, and new parameters, $\vec{\theta}_\phi$. More specifically, we might choose ϕ to imitate logistic regression:

$$\text{logit}\left(\phi_{\tau'_{1,\rho},\tau'_{1,\rho},t}\right) = \text{logit}\left(\phi\left(\vec{\theta}_\phi, \vec{x}_{\phi,\rho,t}\right)\right) = \theta_{\phi,0} + \sum_k \theta_{\phi,k} x_{\phi,\rho,t,k}.$$

It is possible to describe the recruitment rate R_c in terms of covariates, and it is usually more natural to describe the recruitment rate R_c rather than the entry probability β_c . For example, the recruitment rate for cohorts recruiting after the first survey could be modeled by imitating Poisson regression:

$$\log\left(R_{c_{\tau'_{1,\rho},t}}\right) = \log\left(R\left(\vec{\theta}_R, \vec{x}_{R,\rho,t}\right)\right) = \theta_{R,0} + \sum_k \theta_{R,k} x_{R,\rho,t,k}.$$

Covariates for the $c_{\tau',0}$ cohorts are by definition lacking, and some sort of assumption must be made for them. However, such an assumption is inherently required, and whether explicitly stated or not, has always been required of any model dealing with such data.

There are many applicable hierarchical structures, ranging from random effects to hierarchical Bayes, that can be applied not only to the demographic parameters but also to the observability parameters. For example, we might assume plots surveyed by the same

observer have the same observability probabilities. Ultimately, these are only simple illustrative examples, and suitable models must be formulated for any particular experiment.

Example: *Salix gooddingii*

We apply a relatively simple model to observations of *Salix gooddingii* seedlings along a gravel-bedded restored reach of the Merced River (Chapter III). We use the same $\tau' = \{\tau'_0\} \cup \{\tau'_{1,\rho}\} \cup \{\tau'_{-1,\rho}\}$ described previously, and assume Markovian state transitions. Trees are immobile, simplifying the transition matrix. For this example, we model survivorship during the interval preceding survey t as a trivial function of daily survivorship rates, which are themselves modeled using logistic regression on the maximal flow velocity when inundated, $x_{\phi,\rho,t,1}$, and the maximum depth to groundwater, $x_{\phi,\rho,t,2}$. Similarly, we model recruitment in the interval preceding survey t using Poisson regression on local seed supply, $x_{R,\rho,t,1}$, and the proportion of days the ground surface provided a moist germination environment, $x_{R,\rho,t,2}$. Furthermore, we assume that $\beta_{c_{\tau'_{1,\rho},0}} = \beta_0$ is the same for every plot. Stem observations were classified according to the same $\psi' = \{\psi'_0\} \cup \{\psi'_{1,\rho}\} \cup \{\psi'_{2,\rho}\} \cup \{\psi'_{3,\rho}\} \cup \{\psi'_{4,\rho}\} \cup \{\psi'_{5,\rho}\}$ described previously, with the addition of states $\psi'_{5,\rho}$ for individuals in plots that were not surveyed.

On occasion, stems were mistakenly not surveyed. To facilitate the simulation of comparably incomplete datasets and to illustrate a non-Markovian process, the observation process distinguishes regular observations from an associated survey history, v^+ , that describes when a stem was surveyed:

$$P(\psi|\tau) = P(\check{v}^+(\psi)) P(\psi|\check{v}^+(\psi), \tau),$$

where $\check{v}^+(\psi)$ gives the survey history associated with observation history ψ . Given a survey history, the probability of an observation history is treated as in an HMM:

$$P(\psi|\check{v}^+(\psi), \tau) = \prod_t p_{\check{\psi}'(\psi,t), \check{\tau}'(\tau,t), t}$$

where $p_{\psi'_{5,\rho}, \tau', s} = 1$ and the $\{p_{\psi', \tau', s} | \tau', \psi' \notin \{\psi'_{5,\rho}\}\}$ form a conditional distribution.

All surveys were conducted by a single observer, so we assume observability is consistent regardless of time or location (i.e., $p_{\psi'_{i,\rho}, \tau'_{j,\rho}, t} = p_{i,j} \forall \rho, t$). Observation criteria were such that truly dead stems were never subsequently observed alive (i.e., $p_{1,-1} = 0$). We assume the probability of a survey history, $P(v^+)$, is independent of location, but otherwise treat them as parameters (i.e., $P(v^+) = q_{v^+} \forall \rho$). For modeling purposes, we standardized covariates, but we report de-standardized parameter values for interpretability. All of the equations for this model, $P([y_{\psi^+}] | \beta_0, \bar{\theta}_R, \bar{\theta}_\phi, [p_{i,j}], [q_{v^+}], [x_{R,\rho,t,k}], [x_{\phi,\rho,t,k}])$, are consolidated in an appendix (Supporting Information). Parameters and credible intervals (CI) were estimated with Markov chain Monte Carlo (MCMC). Widely bounded uniform priors were used for β_0 and the standardized regression coefficients and uniform Dirichlet priors were used for the $[p_{i,j}]$ and $[q_{v^+}]$.

Due to the small size of the dataset, posterior distributions are wide (Figures 3.1; 3.S1) and heavily influenced by their priors, and especially the Dirichlet priors. Although the dataset was restricted to individuals that were not observed in the first survey, approximately 6% (2–20%) of these were estimated to have been missed in the first survey. Live individuals were correctly identified as such 90% (79–97%) of the time and missed 4% (0.1–15%) of the time. The recruitment intercept implies a daily recruitment rate of 0.002 m^{-2} (0.0004–0.007 m^{-2}), but the recruitment coefficient $\theta_{R,2}$ implies that plots in which

the proportion of the time the ground surface provided a moist germination environment was increased by 10% experienced an average daily recruitment rate that was increased by a factor of 1.5 (1.3–1.7). The posterior for $\theta_{R,1}$ spans 0, although the posterior mean was positive. The survivorship coefficients, $\vec{\theta}_\phi$, corresponded to effectively perfect survivorship at those plots with observed individuals, and the wide posterior reflects the broad range of parameter values that can produce such a result as well as. As a result, survivorship rates were generally very high, causing the observability of dead stems, $[p_{i,-1}]$, to be especially dominated by the Dirichlet prior. Although 96% of individuals were located in plots that were fully surveyed, the Dirichlet prior and small sample size caused the associated $q_{v_{15}^+}$ to be estimated at 52% (35–69%).

Example: Simulated Datasets

We simulated datasets generated through the process described in the *Salix gooddingii* example, based upon the estimated posterior, but varying the number of plots by 1, 3, 10, and 30 times, the recruitment rate by 10 and 100 times, and the survivorship coefficients to produce more moderate rates (Table 3.S1). Simulated covariates were sampled with replacement from a dataset similar to the observed covariate data. We then examined how effectively we were able to recover those parameter values from the simulated data.

Posteriors reflected simulated parameter values and stochastic variation (Figures 3.1; 3.S1). More plots led to more precise parameter estimates. Elevated recruitment rates effectively increased the sample size, and estimated posteriors were comparable to those derived from an equivalently elevated number of plots. With a larger sample size, there were enough mortality events to begin to estimate the effect of covariates on survivorship. Moderate survivorship drastically increased the relative number of mortality events,

allowing for markedly better estimation of survivorship coefficients, but observability parameters did not change nearly as dramatically.

These simulations illustrate the relationship between demographic rates, sample size, posterior precision, and prior influence. As always, a larger sample size increases the posterior precision, but the effective sample size for a given parameter is also a function of the demographic rates. Higher recruitment rates mean more observed individuals and greater overall precision, but extreme survivorship rates require large sample sizes to reliably estimate. When the sample size is low, priors can dominate, and the uniform Dirichlet prior in particular can induce strong posteriors.

Discussion

The generic hidden process model we have presented combines the core elements of multistate and multievent models with a Poisson recruitment process that is closely related to superpopulation entry probability models. Potential applications encompass those of the component models as well as novel combinations, such as studies of the recruitment rate of populations with multiple states and uncertainty in state assessments. Being drawn from multistate models, it can be applied to stratified populations, such as a mixture of males and females with distinct vital rates or plants at different locations, and it can be applied to populations of individuals that can change state, such as birds migrating among sub-populations or oaks tapping deep groundwater. Incorporating state assignment uncertainty as with multievent models means it can accommodate both assignment errors, such as misidentification of breeders not engaged in characteristic breeding behavior, as well as varying degrees of certainty regarding condition, such as tortoises “observed” in their burrows via radio tags.

By incorporating a Poisson recruitment process, the hidden process model is capable of estimating recruitment rates at different times and locations and how variations in these recruitment rates are related to measured covariates, even when the time of recruitment is uncertain due to imperfect detection, and even in the presence of non-reproductive life stages. The hidden process model with its Poisson recruitment can be reparameterized in terms of seniority rates (Pradel, 1996) or superpopulations and entry probabilities (Schwarz and Arnason, 1996), as all of these models share the same fundamental approach. Nonetheless, population models and general recruitment hypotheses mostly relate to the recruitment rates themselves, and a matching parameterization facilitates construction of suitable models.

As with all other generic capture-recapture models, the generic hidden process model suffers from non-identifiable parameters and can be overfitted. Constraints on the nominal model parameters, such as Markovian transitions, Bayesian priors, and covariates and hierarchical structures, can reduce the degrees of freedom and ensure parameter identifiability. In turn, these constraints are easier to construct when specific mechanisms are hypothesized to affect demographic rates and when experimental protocols, such as robust design (Pollock, 1982), help isolate parameters from each other. For example, when the first detection probabilities differ from those of subsequent detections, recruitment rates and first detection probabilities are not generally identifiable, as low recruitment and high first detection rates cannot be distinguished from high recruitment and low first detection rates. This is particularly relevant for plants, but can also apply to animals with dens or burrows. However, under a robust design, first detection probabilities can be identified due to assumed population closure within the secondary samples. Furthermore, it is sometimes

more important simply to be able to recognize confounded parameters than to obtain precise point estimates, as the remaining identifiable parameter estimates can still be used for inference. Bayesian methods are particularly useful, as these non-identifiable parameters produce ridges in the joint posterior distribution.

Although these capture-recapture models can be very useful, they are subject to both familiar and unexplored limitations. For example, they can be multimodal. The *Salix gooddingii* model remains identifiable if we relax the assumption that truly dead stems are never observed alive, but there is a broad secondary mode characterized by high mortality and almost complete misclassification that is also orders of magnitude less likely. This secondary mode can trap maximum likelihood algorithms and require extended burnin for MCMC algorithms. Similarly, the use of regression-like covariate models introduces many familiar regression problems, such as multicollinearity, leverage, autocorrelation, and separability. However, there is ample future work to be done exploring how severely these affect capture-recapture models and how to account or adjust for them.

The factored form of the hidden process model, $P([y_{\psi^+}])$, simply marginalizes the auxiliary variables, $n_{\tau,\psi}$, and the multinomial form of the factored likelihood, with truncated probabilities $P^+(\psi^+)$, generalizes the likelihoods used by most existing capture-recapture models. Like traditional capture-recapture models, this factored likelihood assumes demographic rates, such as survivorship, do not depend on the total population size. By marginalizing the auxiliary $n_{\tau,\psi}$, population sizes are not explicitly estimated, but the population size for a particular time, location, life stage, or combination of such follows a mixture distribution of Poisson distributions for the n_{τ,ψ^-} and binomial distributions derived from the multinomially distributed $[n_{\tau|\psi^+}]$, all of which are restricted to the relevant fates τ .

As we have demonstrated, standard hidden Markov capture-recapture models are a special case of this hidden process model, and not all of the strong assumptions of hidden Markov models are strictly necessary. For example, hidden Markov models by definition assume that each observation depends only on the current state of the individual and not on any of its prior states or observations, but violations of this assumption are common, such as when capture probabilities are influenced by previous captures or when observers are biased by knowledge of their previous assessments. The hidden process model makes it clear that likelihoods for models accommodating such situations are as simple as writing suitable R_c , $P(\tau|c)$, and $P(\psi|\tau)$.

Using the models we have presented, it is possible to explore the relationship between environmental covariates and recruitment and survivorship rates in a wider range of datasets than previously. Unlike previous models, the models presented here can estimate the influence of covariates upon recruitment rates in populations with multiple states and uncertain state assessments. These models combine multistate and multievent models with a Poisson recruitment process that is more directly applicable to ecological hypotheses of recruitment while still being closely related to superpopulation entry probability and seniority probability models. Although we have examined these models through an example dataset of plants, they apply equally well to animals. More broadly, these models continue a shift towards describing the relationship between explanatory covariates and survivorship rates (Lebreton et al., 1992) and recruitment rates (Schwarz and Arnason, 1996). Furthermore, they propagate a growing recognition that most capture-recapture models share many of the same fundamental population processes and can be combined to broaden their applicability. However, there are many avenues for future work, such as continuous

observation distributions, continuous state spaces, and existing approaches to individual heterogeneity.

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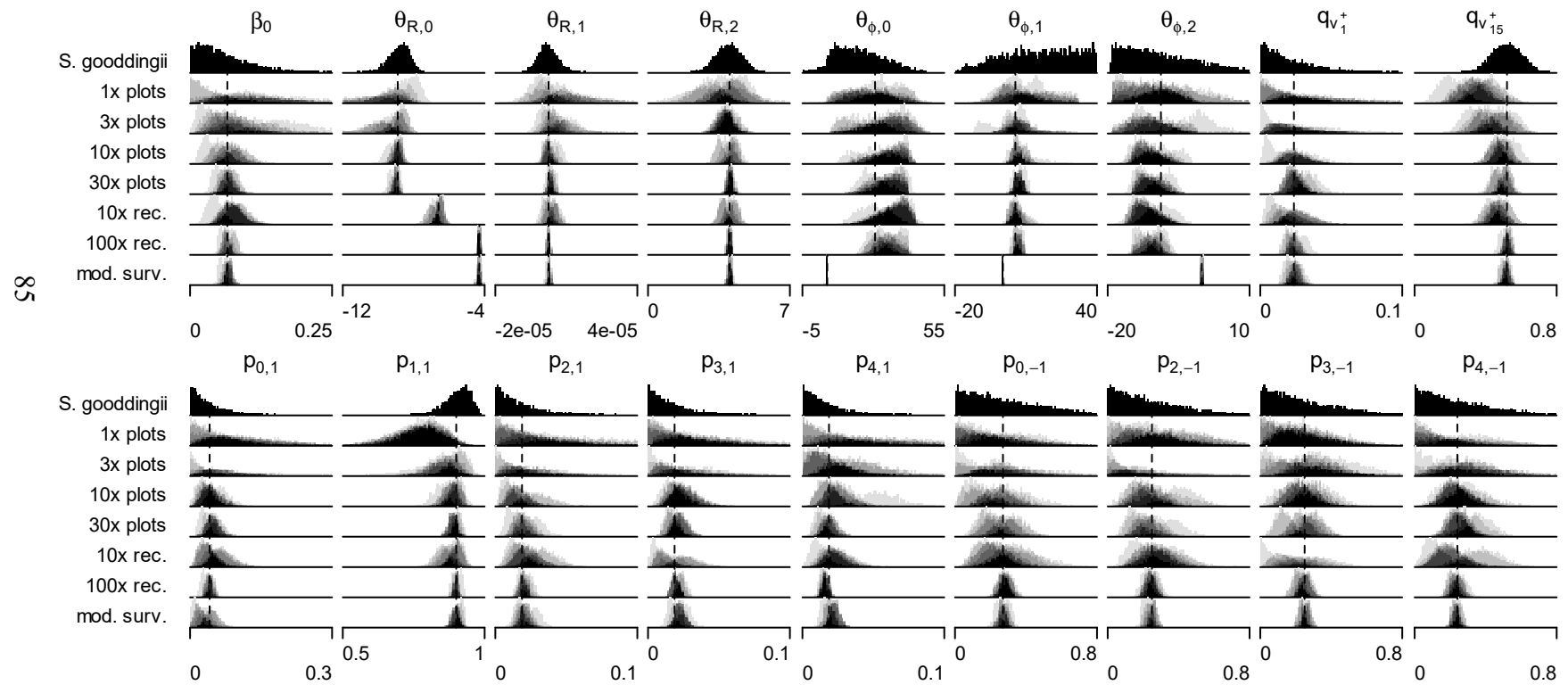
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Figures

Figure 3.1. Select estimated posteriors. For simulations, dashed lines indicate true parameter values and darker shades indicate agreement among replicates. Posteriors for $q_{v_2^+}$ through $q_{v_{14}^+}$ are largely indistinguishable from $q_{v_1^+}$.



Supporting Information

Factored Hidden Process Model

Central to the hidden process model is the likelihood of a particular possible reality:

$$P([n_{\tau,\psi}]) = \prod_c \mathbb{P}(n_c | R_c) \mathbb{M}([n_{\tau|c}] | [P(\tau|c)]) \prod_{\tau \in \tau_c} \mathbb{M}([n_{\psi|\tau}] | [P(\psi|\tau)]).$$

The product of a Poisson and a multinomial likelihood is a product of Poisson likelihoods.

Therefore, we may simplify $P([n_{\tau,\psi}])$:

$$\begin{aligned} P([n_{\tau,\psi}]) &= \prod_c \mathbb{P}(n_c | R_c) \mathbb{M}([n_{\tau|c}] | [P(\tau|c)]) \prod_{\tau \in \tau_c} \mathbb{M}([n_{\psi|\tau}] | [P(\psi|\tau)]) \\ &= \prod_c \prod_{\tau \in \tau_c} \mathbb{P}(n_{\tau|c} | R_c P(\tau|c)) \mathbb{M}([n_{\psi|\tau}] | [P(\psi|\tau)]) \\ &= \prod_c \prod_{\tau \in \tau_c} \mathbb{P}(n_{\psi|\tau} | R_c P(\tau|c) P(\psi|\tau)) \\ &= \prod_{\tau,\psi} \mathbb{P}(n_{\tau,\psi} | R_{\tau,\psi}) \\ &= \mathbb{P}(N|R) \mathbb{M}([n_{\tau,\psi}] | [P(\tau,\psi)]). \end{aligned}$$

Regarding notation, we use Cartesian products to factor sums of products:

$$\sum_{\mathbf{Z}} x \cdot y = \left(\sum_{\mathbf{X}} x \right) \left(\sum_{\mathbf{Y}} y \right),$$

where x and y are elements of sets \mathbf{X} and \mathbf{Y} , and $\mathbf{Z} = \mathbf{X} \times \mathbf{Y}$.

We factor the set of all possible realities $\mathbf{C} = \mathbf{C}^+ \times \mathbf{C}^-$ into the possibilities for observed individuals, $\mathbf{C}^+ = \{[n_{\tau,\psi^+}] | \psi^+ \in \Psi^+, \sum_{\tau} n_{\tau,\psi^+} = y_{\psi^+}\}$, and the possibilities for unobserved individuals, $\mathbf{C}^- = \{[n_{\tau,\psi^-}] | \psi^- \in \Psi^-\}$. We further factor the set of possibilities for observed individuals $\mathbf{C}^+ = \prod_{\psi^+} \mathbf{C}_{\psi^+}$ into the possibilities for individuals observed with a specific

history, $\mathbf{C}_{\psi^+} = \left\{ [n_{\tau|\psi^+}] \mid \sum_{\tau} n_{\tau|\psi^+} = y_{\psi^+} \right\}$. We similarly factor the set of possibilities for unobserved individuals $\mathbf{C}^- = \prod_{\tau, \psi^-} \mathbf{C}_{\tau, \psi^-}$ into the possibilities for individuals with specific fate-history pairs, $\mathbf{C}_{\tau, \psi^-} = \{n_{\tau, \psi^-}\}$, each of which, being unobserved and unconstrained, is simply the set of non-negative integers. As long as none of the $P(\psi|\tau)$, $P(\tau|c)$, or R_c depend on the $n_{\tau, \psi}$, we may factor the integrated likelihood:

$$\begin{aligned}
P([y_{\psi^+}]) &= \sum_{\mathbf{C}} \prod_{\tau, \psi} \mathbb{P}(n_{\tau, \psi} | R_{\tau, \psi}) \\
&= \left(\sum_{\mathbf{C}^+} \prod_{\tau, \psi^+} \mathbb{P}(n_{\tau, \psi^+} | R_{\tau, \psi^+}) \right) \cdot \left(\sum_{\mathbf{C}^-} \prod_{\tau, \psi^-} \mathbb{P}(n_{\tau, \psi^-} | R_{\tau, \psi^-}) \right) \\
&= \left(\prod_{\psi^+} \sum_{\mathbf{C}_{\psi^+}} \prod_{\tau} \mathbb{P}(n_{\tau|\psi^+} | R_{\tau, \psi^+}) \right) \cdot \left(\prod_{\tau, \psi^-} \sum_{\mathbf{C}_{\tau, \psi^-}} \mathbb{P}(n_{\tau, \psi^-} | R_{\tau, \psi^-}) \right) \\
&= \left(\prod_{\psi^+} \sum_{\mathbf{C}_{\psi^+}} \mathbb{P}(y_{\psi^+} | R_{\psi^+}) \mathbb{M} \left([n_{\tau|\psi^+}] \mid \left[\frac{R_{\tau, \psi^+}}{R_{\psi^+}} \right] \right) \right) \cdot 1 \\
&= \prod_{\psi^+} \mathbb{P}(y_{\psi^+} | R_{\psi^+}) \sum_{\mathbf{C}_{\psi^+}} \mathbb{M} \left([n_{\tau|\psi^+}] \mid \left[\frac{R_{\tau, \psi^+}}{R_{\psi^+}} \right] \right) \\
&= \prod_{\psi^+} \mathbb{P}(y_{\psi^+} | R_{\psi^+}) \cdot 1 \\
&= \mathbb{P}(y | R^+) \mathbb{M}([y_{\psi^+}] | [P^+(\psi^+)]).
\end{aligned}$$

Although we derive the truncated multinomial probabilities $P^+(\psi^+)$ through the recruitment rates, they can also be calculated in terms of the relative entry probabilities β_c :

$$P^+(\psi^+) = \frac{R_{\psi^+}}{R^+} = \frac{\sum_{\tau} R_{\tau, \psi^+}}{\sum_{\tau, \psi^+} R_{\tau, \psi^+}} = \frac{R \cdot \sum_{\tau} P(\tau, \psi^+)}{R \cdot \sum_{\tau, \psi^+} P(\tau, \psi^+)} = \frac{\sum_{\tau} P(\tau, \psi^+)}{\sum_{\tau, \psi^+} P(\tau, \psi^+)}.$$

Salix gooddingii Model

For the sake of clarity, we detail the *Salix gooddingii* model and reiterate parameter relationships. First, $\boldsymbol{\rho} = \{\rho_i\}$ is the set of all study sites. The state space $\boldsymbol{\tau}' = \{\tau'_0\} \cup \{\tau'_{1,\rho}\} \cup \{\tau'_{-1,\rho}\}$ consists of individuals that have not yet recruited (τ'_0), are alive at site ρ ($\tau'_{1,\rho}$), or are dead at site ρ ($\tau'_{-1,\rho}$). The observation space $\boldsymbol{\psi}' = \{\psi'_0\} \cup \{\psi'_{1,\rho}\} \cup \{\psi'_{2,\rho}\} \cup \{\psi'_{3,\rho}\} \cup \{\psi'_{4,\rho}\} \cup \{\psi'_{5,\rho}\}$ consists of individuals declared not detected (ψ'_0), alive at site ρ ($\psi'_{1,\rho}$), probably alive at site ρ ($\psi'_{2,\rho}$), probably dead at site ρ ($\psi'_{3,\rho}$), dead at site ρ ($\psi'_{4,\rho}$), or located in a plot that was not surveyed ($\psi'_{5,\rho}$). There were four survey occasions. The model likelihood is based first upon the hidden process model:

$$P([y_{\psi^+}] | \beta_0, \bar{\theta}_R, \bar{\theta}_\phi, [p_{i,j}], [q_{v^+}], [x_{R,\rho,t,k}], [x_{\phi,\rho,t,k}]) = \prod_{\psi^+} \mathbb{P}(y_{\psi^+} | R_{\psi^+})$$

$$R_{\psi^+} = \sum_{\tau} R_{\tau,\psi^+}$$

$$R_{\tau,\psi} = R_{\check{c}(\tau)} P(\tau | \check{c}(\tau)) P(\psi | \tau).$$

We assume Markov state transitions:

$$P(\tau | c) = \prod_{t > \check{r}(\tau)} \phi_{\check{r}'(\tau,t), \check{r}'(\tau,t+1), t}$$

We assume plants do not migrate and dead individuals remain dead. We assume all transition probabilities are 0, except otherwise mentioned:

$$\phi_{\tau'_{-1,\rho}, \tau'_{-1,\rho}, t} = 1$$

$$\phi_{\tau'_{1,\rho}, \tau'_{1,\rho}, t} = \left(\phi_{d, \tau'_{1,\rho}, \tau'_{1,\rho}, t} \right)^{d_{\rho,t}}$$

$$\phi_{\tau'_{1,\rho}, \tau'_{-1,\rho}, t} = 1 - \phi_{\tau'_{1,\rho}, \tau'_{1,\rho}, t}$$

where $\phi_{d,\tau'_{1,\rho},\tau'_{1,\rho},t}$ is the daily survivorship rate between time t and $t + 1$ for an individual in plot ρ and $d_{\rho,t}$ is the number of days between surveys t and $t + 1$ of plot ρ . This daily survivorship rate was treated similarly to logistic regression:

$$\text{logit}(\phi_{d,\tau'_{1,\rho},\tau'_{1,\rho},t}) = \dot{\theta}_{\phi,0} + \dot{\theta}_{\phi,1}\dot{x}_{\phi,\rho,t,1} + \dot{\theta}_{\phi,2}\dot{x}_{\phi,\rho,t,2},$$

where $\dot{x}_{\phi,\rho,t,k}$ is the standardized version of $x_{\phi,\rho,t,k}$ and $\dot{\theta}_{\phi,k}$ is the corresponding coefficient for the standardized covariate. We assume the proportion of pre-existing individuals is the same regardless of plot and that no dead individuals recruit:

$$R_{c_{\tau'_{1,\rho},0}} = \frac{\beta_0}{1 - \beta_0} \sum_{t>0} R_{c_{\tau'_{1,\rho},t}}$$

$$R_{c_{\tau'_{-1,\rho},0}} = 0$$

$$\log(R_{c_{\tau'_{1,\rho},t}}) = \dot{\theta}_{R,0} + \dot{\theta}_{R,1}\check{x}_{R,\rho,t,1} + \dot{\theta}_{R,2}\check{x}_{R,\rho,t,2}.$$

We assume observations do not depend on time or location and that truly dead stems were never observed alive. The observation process distinguishes the regular observation history from the survey history (Table 3.S2):

$$P(\psi|\tau) = P(\check{v}^+(\psi)) P(\psi|\check{v}^+(\psi), \tau)$$

$$P(\psi|\check{v}^+(\psi), \tau) = \prod_t p_{\check{\psi}'(\psi,t), \check{x}'(\tau,t), t}$$

$$p_{\psi'_{i,\rho}, \tau'_{j,\rho}, t} = p_{i,j}$$

$$p_{\psi'_{0,\rho}, \tau'_{j,\rho}, t} = p_{0,j}$$

$$p_{\psi'_{i,\rho}, \tau'_{0,\rho}, t} = 0$$

$$p_{\psi'_{0,\rho}, \tau'_{0,\rho}, t} = 1$$

$$p_{1,-1} = 0$$

$$P(v^+) = q_{v^+}.$$

Covariate data were centered and scaled for analysis:

$$\dot{x}_{i,\rho,t,k} = \frac{x_{i,\rho,t,k} - \bar{x}_{i,k}}{s_{i,k}},$$

where $\bar{x}_{i,k}$ is the mean over plots and times and $s_{i,k}$ is the corresponding sample standard deviation. Untransformed parameter estimates were extracted for presentation:

$$\theta_{i,k} = \frac{\dot{\theta}_{i,k}}{s_{i,k}} \quad \forall k > 0$$

$$\theta_{i,0} = \dot{\theta}_{i,0} - \sum_{k>0} \frac{\dot{\theta}_{i,k} \bar{x}_{i,k}}{s_{i,k}}.$$

Finally, we utilize uninformative priors:

$$\beta_0 \sim \mathbb{U}(0,1)$$

$$\check{\theta}_{R,k} \sim \mathbb{U}(-25,5)$$

$$\check{\theta}_{\phi,k} \sim \mathbb{U}(-25,25)$$

$$[p_{i,1}] \sim \mathbb{D}(\vec{\mathbb{1}})$$

$$[p_{i \neq 1, -1}] \sim \mathbb{D}(\vec{\mathbb{1}})$$

$$[q_{v^+}] \sim \mathbb{D}(\vec{\mathbb{1}}),$$

where \mathbb{U} indicates the uniform distribution, \mathbb{D} indicates the Dirichlet, $\vec{\mathbb{1}}$ is a suitably sized ones vector, and $[p_{i \neq 1, -1}]$ is the sub-vector of $[p_{i, -1}]$ without the element $p_{1, -1}$.

Supporting Tables

Table 3.S1. Simulation true parameter values. Bolded values differ from the 1x plots simulation.

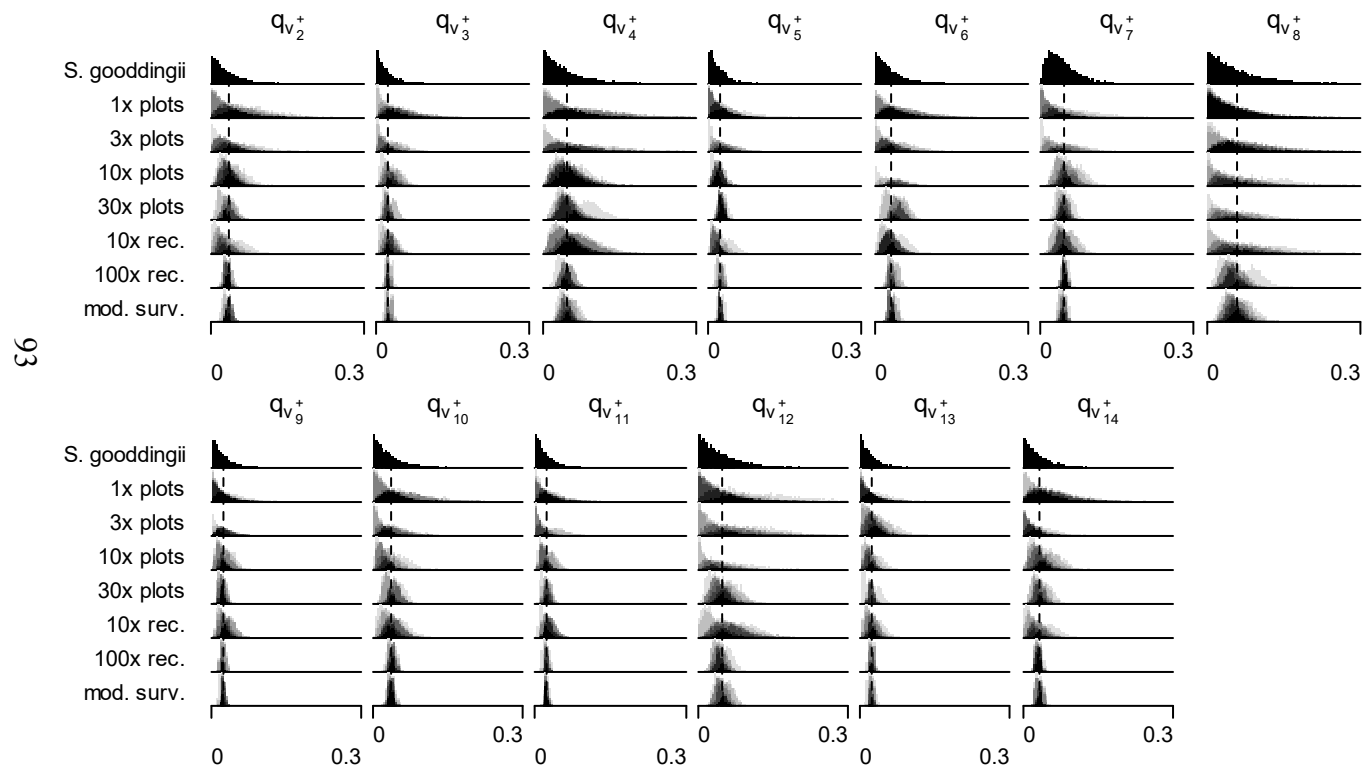
parameter	1x plots	3x plots	10x plots	30x plots	10x rec.	100x rec.	mod. surv.
# plots	23600	70800	236000	708000	23600	23600	23600
β_0	0.0674	0.0674	0.0674	0.0674	0.0674	0.0674	0.0674
$\theta_{R,0}$	-8.91	-8.91	-8.91	-8.91	-6.61	-4.3	-4.3
$\theta_{R,1}$	2.67E-06	2.67E-06	2.67E-06	2.67E-06	2.67E-06	2.67E-06	2.67E-06
$\theta_{R,2}$	3.96	3.96	3.96	3.96	3.96	3.96	3.96
$\theta_{\phi,0}$	26.3	26.3	26.3	26.3	26.3	26.3	5.5
$\theta_{\phi,1}$	5.49	5.49	5.49	5.49	5.49	5.49	0.2
$\theta_{\phi,2}$	-8.89	-8.89	-8.89	-8.89	-8.89	-8.89	-0.2
$p_{0,1}$	0.0414	0.0414	0.0414	0.0414	0.0414	0.0414	0.0414
$p_{1,1}$	0.903	0.903	0.903	0.903	0.903	0.903	0.903
$p_{2,1}$	0.0189	0.0189	0.0189	0.0189	0.0189	0.0189	0.0189
$p_{3,1}$	0.0186	0.0186	0.0186	0.0186	0.0186	0.0186	0.0186
$p_{4,1}$	0.0186	0.0186	0.0186	0.0186	0.0186	0.0186	0.0186
$p_{0,-1}$	0.269	0.269	0.269	0.269	0.269	0.269	0.269
$p_{2,-1}$	0.244	0.244	0.244	0.244	0.244	0.244	0.244
$p_{3,-1}$	0.243	0.243	0.243	0.243	0.243	0.243	0.243
$p_{4,-1}$	0.244	0.244	0.244	0.244	0.244	0.244	0.244
$q_{v_1^+}$	0.0235	0.0235	0.0235	0.0235	0.0235	0.0235	0.0235
$q_{v_2^+}$	0.0348	0.0348	0.0348	0.0348	0.0348	0.0348	0.0348
$q_{v_3^+}$	0.0231	0.0231	0.0231	0.0231	0.0231	0.0231	0.0231
$q_{v_4^+}$	0.0482	0.0482	0.0482	0.0482	0.0482	0.0482	0.0482
$q_{v_5^+}$	0.0232	0.0232	0.0232	0.0232	0.0232	0.0232	0.0232
$q_{v_6^+}$	0.034	0.034	0.034	0.034	0.034	0.034	0.034
$q_{v_7^+}$	0.0455	0.0455	0.0455	0.0455	0.0455	0.0455	0.0455
$q_{v_8^+}$	0.0587	0.0587	0.0587	0.0587	0.0587	0.0587	0.0587
$q_{v_9^+}$	0.0235	0.0235	0.0235	0.0235	0.0235	0.0235	0.0235
$q_{v_{10}^+}$	0.0341	0.0341	0.0341	0.0341	0.0341	0.0341	0.0341
$q_{v_{11}^+}$	0.0229	0.0229	0.0229	0.0229	0.0229	0.0229	0.0229
$q_{v_{12}^+}$	0.0484	0.0484	0.0484	0.0484	0.0484	0.0484	0.0484
$q_{v_{13}^+}$	0.0233	0.0233	0.0233	0.0233	0.0233	0.0233	0.0233
$q_{v_{14}^+}$	0.0338	0.0338	0.0338	0.0338	0.0338	0.0338	0.0338
$q_{v_{15}^+}$	0.523	0.523	0.523	0.523	0.523	0.523	0.523

Table 3.S2. Survey histories enumerated.

v^+	survey			
	1	2	3	4
v_1^+	not	not	not	surveyed
v_2^+	not	not	surveyed	not
v_3^+	not	not	surveyed	surveyed
v_4^+	not	surveyed	not	not
v_5^+	not	surveyed	not	surveyed
v_6^+	not	surveyed	surveyed	not
v_7^+	not	surveyed	surveyed	surveyed
v_8^+	surveyed	not	not	not
v_9^+	surveyed	not	not	surveyed
v_{10}^+	surveyed	not	surveyed	not
v_{11}^+	surveyed	not	surveyed	surveyed
v_{12}^+	surveyed	surveyed	not	not
v_{13}^+	surveyed	surveyed	not	surveyed
v_{14}^+	surveyed	surveyed	surveyed	not
v_{15}^+	surveyed	surveyed	surveyed	surveyed

Supporting Figures

Figure 3.S1. Estimated posteriors for $q_{v_2^+}$ through $q_{v_{14}^+}$. For simulations, dashed lines indicate true parameter values and darker shades indicate agreement among replicates.



4. Patterns and Predictors of Recruitment of Three Riparian Salicaceae along a Gravel-bedded Mediterranean-climate River

Introduction

Under Mediterranean climates, riparian zones are distinctly mesic and have higher summer primary productivity rates than adjacent habitats, and this productivity supports wildlife in both terrestrial and aquatic ecosystems (Knopf et al. 1988, Naiman & Decamps 1997). However, the extent of riparian forests has decreased along many rivers. For example, of the riparian forests estimated to exist along the Sacramento River in 1848, less than 2% remain, due largely to land clearing (Roberts et al. 1977). Much of the remaining riparian forests has been degraded by dams and water extraction. Cottonwoods and willows are especially sensitive to changes in the timing, magnitude, and recession rate of floods, and alterations due to flow regulation can cause recruitment failure (Rood & Mahoney 1990).

Riparian cottonwoods and willows are pioneer species whose recruitment depends on the timing of seed release and flooding and the location of germination beds within the channel (Figure 4.1; Scott et al. 1993, Mahoney & Rood 1998, Shafroth et al. 1998). The seed release period for these species is narrow and typically coincides with the recession of spring floods, derived from seasonal storms and snowmelt. Large quantities of wind- and water-dispersed seeds are deposited on freshly deposited moist and bare sediment surfaces (Braatne et al. 1996, Karrenberg et al. 2002). Seeds demonstrate no dormancy and germinate readily when exposed to moisture (Fenner et al. 1984), even in the absence of substrate (Hosner 1957). These species are phreatophytic, and the roots of the newly emerged seedlings follow the declining groundwater table. Should groundwater decline too

quickly, the seedlings will be unable to keep their roots in the moist capillary fringe. Germinants that establish too high above the river are stranded and killed by drought, while those that establish too low in the channel are scoured in subsequent years. In short, successful recruitment occurs when seed release coincides with flooding of sufficient magnitude and moderate recession rate so that germinating seedlings can avoid late-season desiccation and scouring in subsequent years.

Field studies of cottonwoods and willows have almost ubiquitously observed dense cohorts of seedlings that experience low survivorship rates. Seedling densities are typically 10–500 m⁻² (McBride & Strahan 1984, Sacchi & Price 1992, Rood et al. 1998, Stella 2005, Polzin & Rood 2006), and successful first-summer survivorship can be as “high” as 2% (Rood et al. 2003). Dense seedling cohorts need not occur every year (e.g., Stromberg et al. 1991), but successful recruitment has been considered unlikely with low survivorship rates. However, naturally-established cottonwoods and willows ranging from seedlings to mature individuals occur along the Robinson Reach of the Merced River even though densities of new germinants consistently appeared atypically low (pers. obs.), suggesting unusually high survivorship rates.

It is not clear whether these seemingly unusual demographic rates are a product of recent restoration activities, peculiarities of local flow regulation, or a previously unobserved capacity for recruitment. To understand why germination and survivorship rates were low along the Robinson Reach, we surveyed seedlings and small individual trees of *Populus fremontii*, *Salix exigua*, and *Salix gooddingii* and measured relevant covariates. In particular, we asked whether germination rates were constrained by seed release, seed arrival, or the availability of moist germination beds and whether mortality rates were

correlated with light levels, groundwater depth, groundwater recession rates, and shear stresses during peak flows.

Methods

Study Site and Species

The Robinson Reach (lat 37°29'30"N, long 120°29'30"W) of the Merced River is 3.2 km long and is located near Merced, California (Figure 4.2). The climate is Mediterranean, with mean monthly temperature ranging from 2 °C in December to 36 °C in July. Between November and March, total normal precipitation is 26 cm, or 80% of the annual total. Along the alluvial reach of the Merced River, in the Central Valley, streamflows are generated by winter rains and snowmelt from the Sierra Nevada mountains. Upstream of the Robinson Reach are the New Exchequer and McSwain dams, which regulate river flows along with a number of public and private diversions. Flows through 2010 were never overbank, although several fall flows were unnaturally timed, but 2011 had a 6 year flood (Figure 4.3).

Typical floodplains are complex mosaics of geomorphic surfaces, but the Robinson Reach has been highly simplified. Historically mined for gravel, the reach was restored beginning in 2001 for the purpose of improving salmon spawning habitat. As part of the process, the channel and floodplain were almost entirely rebuilt at a scale consistent with the prevailing modern flow regime. Although fill material originated from on-site, the particle size distribution of the restored floodplain is much more spatially homogeneous than that produced by fluvial processes. Vertical soil profiles are similarly simplified and lack surficial sandy silts that are normally deposited from suspension by overbank flows in the region. In other words, parts of the floodplain that one might typically expect to differ in

topography and soil characteristics do not actually differ. The historical legacies inherent to floodplain genesis have been eliminated in the process of rapid engineering, and this simplification reduces the impact of variations in substrate on recruitment.

Woody vegetation along the Robinson Reach was composed of species typical of the region, but at lower densities than nearby unrestored areas (pers. obs.). The focal species of this study were the local dominants, *Populus fremontii*, *Salix gooddingii*, and *Salix exigua*. *Alnus rhombifolia*, *Acer saccharinum*, and suspected hybrids of *Platanus racemosa* and *Platanus ×hybrida* were also commonly encountered, while *Quercus lobata*, *Fraxinus latifolia*, *Morus alba*, *Acer negundo*, *Salix laevigata*, and *Salix lasiolepis* were less frequently encountered. Patches of relictual vegetation were deliberately preserved as seed sources during floodplain construction activities, but both relictual patches and revegetation efforts were generally limited to the floodplain beyond the immediate channel margins examined in this study, and mature vegetation remained sparse.

Data

Woody vegetation was surveyed 5 times along 76 monumented 1×25 m transects beginning within the channel and extending onto the floodplain. However, groundwater elevations could only be interpolated at 59, so we only present stem survey data from those 59 transects. Transects were gridded into square plots 0.25 m on a side, and within each plot, all stems of all species were marked and recorded. Stems as small as 5 cm were observed. The initial survey was conducted in October 2009. To distinguish mortality due to overwintering, spring floods, and summer drought, subsequent surveys were conducted in April, July, and October 2010 (Figure 4.3). Then due to weeks of continuous overbank flooding in 2011, the final survey was delayed until November 2011, when only 38 transects

were surveyed. This paper focuses on stems first observed in the smallest height class (<1 m), which were partitioned into small individuals, which were observed in the first survey, and “seedlings”, which were not observed in the first survey. Due to ambiguity introduced by phenology and also by beavers, stems were classified as alive, probably alive, probably dead, and dead every time they were observed. Transects were classified as beginning on point bars, cut banks, or the intervening riffle banks.

To estimate the seed release period, 188 potential mother trees were selected in March 2010 using point-centered sampling. They were subsequently monitored every 2 weeks (Figure 4.3). Open catkins in the top, middle, and bottom portions of the crowns were counted with binoculars for 20 seconds per portion. For each mature female, the total open catkins were linearly interpolated to a daily resolution. A daily sitewide seed release index was calculated by averaging across mature females. Because of flooding, no covariate data, seed release or otherwise, were collected after 2010.

Wind and water dispersal were measured at 12 of the vegetation transects. At each of these transects, there was one wind-dispersal seed trap, which consisted of a bucket with a 730 cm² opening filled with roughly 30 cm of water and covered with a coarse screen to exclude animals. Seedlings were collected and the buckets cleaned and refilled every 2 weeks (Figure 4.3). Collected seedlings were transplanted into flats and grown until they could be identified, but seedlings collected before June 2010 died before becoming identifiable due to watering problems, and are not further discussed. Parallel to and 5 m downstream of each of the 12 transects, a transect of textured-mat seed traps was installed to measure water dispersal. Each water-dispersal transect consisted of 3–12 mats, each 100 cm² in size, positioned every 2 m from the low-flow edge of the river to just beyond the

bankfull margin. Mats were placed on April 15, 2010, prior to spring floods, and retrieved on June 24, 2010, following flood recession. The mats were germinated in a greenhouse and seedlings grown until identifiable.

Illuminance at the ground surface as a proportion of full sunlight was used as a measure of the shading and competition experienced by seedlings. Ground surface measurements were made at 1 m intervals along the vegetation transects using an Extech EasyView EA30 light meter. To compensate for clouds and time of day, full sunlight control measurements were taken at the beginning and end of each transect and as deemed necessary. Although relative illuminance as a proportion of full sunlight is less sensitive to the time of day than absolute illuminance, measurements were taken within 2–3 hours of solar noon, depending on season. Light surveys were conducted at all transects concurrently with the vegetation surveys and additional surveys were conducted at the seed trap transects concurrently with the sampling of the wind-dispersal seed traps (Figure 4.3). Due to angle effects, spatially adjacent measurements were averaged. These smoothed values were linearly interpolated along the transect and then through time before being averaged to produce a light index for each plot and between-survey interval.

Shear stresses during peak flow events were estimated from approximately 1 m resolution simulations of the MD-SWMS hydrologic model at discharges of 32.6 and 42.5 m³/s (Harrison et al. 2011). Daily discharge was recorded 3 km upstream of the study site by the California Department of Water Resources at the Merced River near Snelling (MSN) gage (Figure 4.3). Daily water surface extents were modeled using HEC-RAS and validated against both MD-SWMS modeled extents as well as high resolution aerial imagery.

Groundwater levels were monitored every 2 weeks from April 2010 through October 2010 (Figure 4.3) at a set of 8 shallow (<4 m) observation wells situated 8–14 m from the bankfull channel margin. When wells were dry, groundwater levels were assumed to be at least the depth of the well. Groundwater surface elevations were estimated by linearly interpolating well observations as a function of date and distance along and from the river and then interpolating from the modeled water surface extents. A lower bound on the depth to groundwater was estimated using the interpolated groundwater surface elevations and a high resolution digital elevation model. The average stressful groundwater elevation change rate was calculated as the average over the interval between surveys of the daily groundwater elevation change rate, after having been smoothed over 3 days (Rood & Mahoney 2000) and with non-stressful smoothed groundwater elevations changes, defined as those above -2.5 cm/day (Mahoney & Rood 1998), set to 0.

On a daily basis, plots were assigned to one of four soil moisture categories defined by the depth to groundwater. In a mixture of sand and gravel, plots with shallow groundwater less than 0.5 m below the ground surface can have a capillary fringe that reaches the ground surface (Mahoney & Rood 1992), and they can provide a distinctly different germination environment from plots with deeper groundwater (Mahoney & Rood 1998) or plots that were underwater. The last category was for those days the groundwater surface was not estimated due to gaps in the discharge data.

Modeling

Because of uncertainty in the fate of unobserved individuals and ambiguity in stem condition, we used a capture-recapture model with Poisson recruitment based upon that presented in Chapter III to estimate spatial and temporal variations in germination/initial

establishment and survivorship rates along with their relationship to seed release, seed arrival, moist germination beds, light levels, groundwater depth, groundwater change rates, and flow-induced shear stresses. Seedlings and small individuals were analyzed separately. Only the 59 transects within the groundwater interpolation region were modeled. Notation has been summarized in Tables 4.1 and 4.S1.

After the first survey, the germination/initial establishment rate was modeled as the product of transect- and survey-specific seed arrival rates and transect- and survey-specific germination fractions, whereas the probability that an individual existed prior to the first survey, β_0 , was assumed to be equal for every plot. The transect- and survey-specific seed arrival rates were modeled as the product of a survey-specific but spatially-averaged sitewide seed arrival rate and transect-specific dispersal factors describing persistent spatial variations in the seed arrival rates. The survey-specific but spatially-averaged sitewide seed arrival rate was modeled as a log-linked linear function, with coefficients $\theta_{S,0}$ and $\theta_{S,1}$, of a survey-specific sitewide seed release index. This survey-specific sitewide seed release index was calculated by totaling the daily sitewide seed release index for each survey period. The survey-specific sitewide seed release index and values derived from it actually varied by transect due to differences in survey dates, but due to the relative unimportance of this variation, the relevant model specifics are deferred to the Supporting Information. The wind-dispersal seed trap observations were assumed to be Poisson distributed samples of equivalently-calculated transect- and survey-specific seed arrival rates, only based upon a survey-specific sitewide seed release index totaled over the seed trap survey periods. The transect-specific dispersal factors were treated hierarchically as parameters drawn from a common gamma-distributed prior with mean 1 and shape parameter α_D , and were

analytically integrated out of the modeled posterior (Supporting Information). The germination fraction was a zero-intercept linear function of the relative duration of each soil moisture category at each plot and between-survey interval, with coefficients $\theta_{w,1}$ through $\theta_{w,4}$.

Five types of models were analyzed, varying in the formulation of survivorship. The first fit a uniform daily survivorship rate from October 2009 to October 2010, ϕ_{2010} , and a separate uniform daily survivorship rate from October 2010 to November 2011, ϕ_{2011} , and is the only one of the five models that can be interpreted when survivorship is 100%. The other four modeled the daily survivorship rate from October 2009 to October 2010 as a univariate logistic regression with intercept $\theta_{\phi,0}$ and varied by the predictor covariate and were intended to examine whether there was any relationship between the covariate and survivorship. These four models fit survivorship relative to shear stress during peak flows with coefficient $\theta_{\phi,1}$ or relative to the maximal depth to groundwater with coefficient $\theta_{\phi,2}$ or relative to the average stressful groundwater elevation change rate with coefficient $\theta_{\phi,3}$ or relative to the light index with coefficient $\theta_{\phi,4}$. Covariates were not measured from October 2009 to April 2010, as the existing literature indicated only shear stress should have been relevant and flows were minimal during this period, so minimally stressful default values of 0 were assigned for all covariates during this period, except a minimally stressful default of 1 was assigned for light.

Model observability parameters, $p_{i,j}$, were assumed not to vary by location or time, and the observation criteria were such that no dead stem should ever have been misclassified as alive. Similarly, survey history probabilities, q_{v^+} , were assumed not to vary by location. Parameter estimates and credible intervals were obtained through Markov Chain Monte

Carlo, a Bayesian method that produces posterior probability distributions, which describe the probability that a parameter has a certain value. A uniform Dirichlet prior was used for the observability parameters and survey history probabilities, which define categorical distributions. Widely bounded uniform priors were used for all other parameters.

Convergence was assessed using the potential scale reduction factor and effective sample size ($\hat{R} < 1.1$ and $\hat{n}_{eff} > 1000$; Gelman et al. 2014). For brevity, further details are deferred to the Supporting Information.

Results

A total of 45 *Populus fremontii*, 34 *Salix exigua*, and 100 *Salix gooddingii* individuals were ever observed in the woody vegetation transects, of which 5, 2, and 23, respectively, were identified as seedlings and 25, 3, and 47 were small but had established prior to 2010. Out of all seedlings and small individuals, only 5 *Populus fremontii*, 0 *Salix exigua*, and 2 *Salix gooddingii* were found beyond the bankfull channel. *Populus fremontii* was rarely found on point bars, which were dominated instead by *Salix exigua*, while *Salix gooddingii* was found nearly everywhere (Table 4.2). Point bars did not seem to be favorable germination/initial establishment sites in 2010, as there were few seedlings. At the same time, however, the largest individuals and the bulk of the observed *Salix exigua* were found on point bars, suggesting they were at one point suitable for recruitment.

Seed release was surveyed at 19 *Populus fremontii*, 42 *Salix exigua*, and 65 *Salix gooddingii* mature females. The mean pattern of seed release (Figure 4.4) was typical of the region (Stella et al. 2006) and in approximate alignment with estimated pre-dam flows (Figure 4.3). However, this overall mean pattern was produced by a mix of early-releasing

individuals, late-releasing individuals, and individuals spanning the entire period with one or two peaks.

Out of 859 seedlings collected from the wind-dispersal seed traps, 161 were identified as *Salix exigua*, 259 as *Salix gooddingii*, 0 as *Populus fremontii*, and 50 did not survive long enough to be identified to species or excluded as irrelevant. Temporal patterns of seed arrival roughly correspond with seed release, although paradoxically, peak seed arrival seemed to precede peak seed release (Figure 4.4). There were two seed arrival peaks for *Salix gooddingii*. Seed arrival rates were much higher at some transects than others (Figure 4.5). There were no seedlings of any of the target species in the water-dispersal seed traps, although there were a number of herbaceous species typical of the riparian zone, often deposited in mobilized sediment.

A range of survivorship covariate values were observed across all plots (Table 4.3), but seedlings and small individuals of all species occurred under similar mild conditions (Figure 4.6). Competing vegetation rendered inundated plots generally darker, but there were some open near-channel environments as well as patches of dense herbaceous ground cover farther from the channel. Seedlings were observed under a wide range of illuminations, ranging from 1–88%. Prior to the 2011 flooding, there were four distinct flow events, with the longest being the spring 2010 flow release and the greatest daily discharge occurring in September 2010 (Figure 4.3). Seedlings experienced shear stresses up to 26 Pa, which were insufficient to mobilize the banks of very coarse gravels (Harrison et al. 2011). Along the Robinson Reach during the period studied, the Merced was a losing river and hence had groundwater elevations that declined with distance from the river. Seedlings were only found where the maximal groundwater depth did not exceed 1.1 m at any point in the year,

which only occurred within the bankfull channel. Similarly, seedlings were only found where the average stressful groundwater elevation change rate was greater than -3 cm/day.

Because so few seedlings of the other species were observed, only *Salix gooddingii* was modeled. Furthermore, when *Salix gooddingii* seedlings were observed in 2010, they were observed alive, so only the average survivorship model could be meaningfully interpreted (Figures 4.7, 4.S1). Live *Salix gooddingii* seedlings were rarely missed, but there was a lingering possibility that some “seedlings” were actually older. Dead seedlings were most likely to be either missed or observed as “probably dead”. Although the individual transect-specific dispersal factors were integrated out of the final model, their distribution was characterized by many small and a few large values. Notably, the *Salix gooddingii* seedling germination/initial establishment rate was increased most by the proportion of days spent underwater, $\theta_{w,2}$, followed by the proportion of days with shallow groundwater, $\theta_{w,3}$, with an unknown soil moisture condition, $\theta_{w,1}$, and then with deep groundwater, $\theta_{w,4}$. Nonetheless, these germination and initial establishment rates indicate very few dispersed propagules established. However, those seedlings that did establish experienced high survivorship rates in 2010, ϕ_{2010} . Seedling survivorship was noticeably lower in 2011, ϕ_{2011} , although this includes both the first winter and an unnaturally long overbank flood generated by reservoir management needs.

Because the survivorship regression models for small *Salix gooddingii* individuals produced similar results (Figures 4.8, 4.S2- 4.S5), we present here only results for the maximal groundwater depth model. The posteriors of the observability parameters for live small individuals were not as strongly influenced by the Dirichlet priors as those for seedlings, but the posteriors were not significantly different. However, dead small

individuals were much more likely to be missed. Again, survivorship rates were higher in 2010 than in 2011. Survivorship in 2010 was strongly delineated by season (Figures 4.9, 4.S6), with winter survivorship rates distinctly lower, despite the absence of scour and other stressors identified in other studies. Posteriors for the survivorship parameters reflected this seasonal separation and the minimally stressful default covariate values used for the winter of 2010.

Discussion

Compared with prior reports from other rivers (e.g., Strahan 1984), there were very few trees and seedlings along the Robinson Reach, because the Merced channel and floodplain were completely reconstructed in 2001. Except for a few areas left undisturbed by the restoration, all trees in the riparian zone were less than 10 years old at the time of this study. Although the timing of seed release was typical of the region, insufficient seed arrival appeared to limit *Populus fremontii* recruitment. Only *Salix gooddingii* was abundant enough to model population dynamics, but the few seedlings that germinated demonstrated high survivorship. Survivorship rates of small *Salix gooddingii* individuals were significantly lower in winter than during spring and summer.

Germination

Because most Salicaceae only release seeds for a few weeks to a month (Niiyama 1990, Van Splunder et al. 1995, Mahoney & Rood 1998, Gage & Cooper 2005), the precise timing of spring flows is considered essential to successful recruitment (Stella et al. 2006). Both *Salix* species studied here dispersed viable seeds into the seed traps for more than 2 months, suggesting these species are less dependent on the exact dates of flooding. There is some

disagreement over the seed release period for these species (Brock 1994, Amlin & Rood 2002, Stella et al. 2006), which could be caused by some combination of regional differences in environment and genotype (Braatne et al. 1996), as well as differences in observers, methods, and terminology. At the very least, the absence of standardized methods and measures precludes further comparison.

Even though dispersal has not previously been reported to be limiting for these prolific pioneer species, low wind-dispersed seed arrival rates contributed to low germination densities at what would otherwise appear to be suitable recruitment locations at this site. Observed wind-dispersed seed arrival was nonexistent for *Populus fremontii* and low for the *Salix* species relative to other estimates for these and similar species (Table 4.S2; Warren & Turner 1975, Fenner et al. 1985, Gage & Cooper 2005). These low seed arrival rates and the large spatial variation in these rates were likely related to the availability and productivity of mother trees along the Robinson Reach, as arrival rates of willow seeds can decline by an order of magnitude within the first 100 m from a seed source (Gage & Cooper 2005). Ultimately, however, the literature provides little quantitative information on what seed arrival rates are adequate or how dense seed sources must be to provide such adequate dispersal, let alone considerations of spatial configuration, and further research would facilitate management and restoration efforts.

The absence of the study species in the water-dispersal seed traps does not necessarily indicate the absence of hydrochory. Hydrochory differs for buoyant and sinking seeds (Chambert & James 2008), but the study species exhibit both behaviors (Hosner 1957), and reference greenhouse seeds would sometimes float, sink, germinate, and then float again. Mat-based seed traps can capture sinking seeds deposited alongside sediments (e.g., Steiger

et al. 2003), and a number of herbaceous but no study species germinated from such deposited sediments, suggesting seeds of the study species were not commonly entrained in sediments. By contrast, our traps may have been insensitive to the deposition of buoyant propagules, which generally occurs at the edge of the river (Merritt & Wohl 2002). Due to the spacing of the traps and the rapid changes in river discharge, the river's edge was only briefly situated at the seed traps, and propagules may simply have been deposited between the seed traps. In addition, most traps were collected some days after the river had receded, during which time deposited propagules may have experienced fatally inhospitable conditions. Ultimately, anemochory, the various modes of hydrochory, and their relative importance all deserve further study.

Germination rates of *Salix gooddingii* seedlings were higher in plots more frequently subjected to capillary wetting, but were even higher in more frequently inundated plots. Germination rates have been shown to decrease with moisture stress (Fenner et al. 1984), but even though seeds will germinate while floating or underwater (Hosner 1957), seedlings are not expected to establish while inundated. Elevated germination rates in frequently inundated plots could reflect poor estimation of moist germination sites in the zone of capillary wetting. The location of this capillary zone depends on river hydrology, the groundwater table, and floodplain topography and subsurface soil texture. Overestimation of the capillary fringe height or groundwater table would lead to overestimation of the zone of capillary wetting and reduce its predictive strength. However, moist germination environments are located adjacent to the channel, and despite being mechanistically indirect, inundation duration may be usefully correlated when estimates of the zone of capillary wetting are inadequate.

Germination rates for all species can be over 85% in the lab (Stella et al. 2006), but observed rates were 0.3% when plots were underwater and less under other soil conditions, indicating a broad constraint on *Salix gooddingii* recruitment. These field observations had more uncertainty than lab measurements, as observed rates were overestimated by any unobserved hydrochory but underestimated if entangling ground-level vegetation and cobwebs led to overestimation of the dispersal rate. Furthermore, field observations of seedling occurrence include both germination and initial establishment, and seedlings that died prior to becoming potentially observable in at least one survey were indistinguishable from those that failed to germinate. It is also possible we observed an unusual year, although dense germination was not apparent in prior years (pers. obs.). Nonetheless, these germination/initial establishment rates were comparable to the lowest rates observed elsewhere (Table 4.S3; Cooper et al. 1999, Gage & Cooper 2005, Cooper & Andersen 2012). Although germination rates In short, it remains unclear why dispersed seeds failed to initially establish, but it is a significant constraint on the recruitment process that deserves further study.

While assuming a horizontal groundwater table may be suitable for whole-river dam-release management (e.g., Rood et al. 2003), it can oversimplify local conditions. Although some riparian water tables may be closely coupled to river stage and roughly horizontal or gently sloping (e.g., Rood et al. 1995), the Merced water table declined away from the channel steeply enough that assuming a horizontal water table would have overestimated the zone of capillary wetting by roughly 70% near the channel (Supporting Information). Furthermore, this discrepancy is exacerbated in the Robinson Reach, where most of the restored floodplain is a low terrace situated roughly 1 m above base flow. Assuming a

horizontal water table, most of this floodplain appears suitable for germination/initial establishment, whereas the actual water table restricted seedlings to the channel margin. Although a horizontal water table coupled to river stage may be a helpful initial approximation, improved estimates of the zone of capillary wetting should improve estimates of germination/initial establishment rates.

Survivorship

Salix gooddingii seedlings only occurred where scour, groundwater depths, and groundwater change rates were within ranges considered mild by the existing literature, and all of them survived their first growing season and for some, the large 2011 flood as well. Indeed, 2010 survivorship was higher than even the wet no-drawdown controls of experimental drawdown studies (Table 4.S4; Mahoney & Rood 1991, Amlin & Rood 2002, Stella 2005), although field estimates of survivorship are inherently overestimated by those seedlings that germinated but died prior to becoming potentially observable in at least one survey. The high 2010 survivorship rate does not include the seedlings' first winter, which could not be separately estimated due to the 2011 flood but can be comparably high (Cooper et al. 1999). Nonetheless, the observed *Salix gooddingii* seedlings germinated and initially established in apparently hospitable locations, due in large part to the fact that the river is only able to move its gravelly-cobbly bed material at flows of about the 5-year recurrence interval (but did so in the 2011 flood). Many studies have examined rivers with extensive germination, where recruitment is largely dictated by differential survivorship (Rood et al. 1998), but under certain circumstances, germination and initial establishment can be more restrictive than survivorship (Segelquist et al. 1993).

Moderate competition, as measured by shading, did not noticeably inhibit the survivorship of *Salix gooddingii* seedlings, even though the study species are nominally shade intolerant and their recruitment hindered by competition (Sacchi & Price 1992, Friedman et al. 1995). Although locally or ephemerally bright conditions, such as sunflecks, seedling-scale gaps, and phenological gaps in the herbaceous canopy, may have increased measurement error, others have also found that shade is not correlated with mortality under well-watered conditions (Cooper et al. 1999). However, reduced productivity may render seedlings more vulnerable to other stresses (Sacchi & Price 1992). Finally, light levels may not have been representative of other forms of competition, such as for water.

The survivorship rates of small *Salix gooddingii* individuals were high during the growing season, comparable to that of seedlings, but noticeably lower during the winter. For small individuals, the growing season, winter, and annual survivorship rates were higher than reported elsewhere (Rood et al. 1998, Cooper et al. 1999). In these other studies, scouring and desiccation remained major sources of mortality, whereas here, the small individuals occurred under similarly mild conditions as the seedlings. Although ring counts under these conditions can be imprecise, a small sample from near the transects was consistent with high survivorship rates and suggested some of the small individuals may have been somewhat older (4–8 years; Supporting Information) than the second- and third-year cohorts in other studies.

Although similar riparian pioneers are often characterized by seedling pulses and episodic recruitment, *Salix gooddingii* appeared to gradually accumulate small quantities of individuals over the course of several years in a relatively narrow fringe along the Robinson Reach. Specifically, low levels of dispersal, germination, and initial establishment appeared

to limit the number of new seedlings, but those seedlings established under mild conditions comparable to those described by previous studies as being tolerable (Mahoney & Rood 1998), leading to unusually high survivorship. In particular, the absence of meaningful scour rendered moist plots low within the channel especially hospitable, even in the presence of low to moderate competition as inferred from light levels. For comparison, recruitment can occur during prolonged periods of diminished scour (Scott et al. 1996), such as that which often follows dam construction (Williams & Wolman 1984). Indeed, channel narrowing may already be occurring, as larger willows were present within the channel, concentrated on but not exclusive to point bars. Many natural habitats, such as backwaters, ponds and lakes, and low order tributaries, are similarly infrequently scoured, and many managed rivers will be for the foreseeable future. Further research is needed to determine how many fringing forests originate through similarly non-pulsed recruitment dynamics.

Conclusions

While these results were generally consistent with previously identified physiological constraints on the recruitment of these species, the resulting recruitment dynamics were quite different, with implications for restoration and management strategies. Although none of the study species are considered dispersal limited, seed arrival rates were low, and it remains unclear how few seed sources is too few. Low levels of *Salix gooddingii* germination/initial establishment were due in part to limited seed release and arrival, but seedlings experienced correspondingly low mortality rates due to perennial moisture and diminished scour at low elevations within the channel. Low germination and mortality rates together suggest gradual accumulation and may help explain the fringing forests commonly lining managed rivers. Although many have studied how recruitment occurs on rivers where

germination and mortality rates are high, recruitment can also occur under other conditions, such as reduced scouring induced by flow regulation.

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Tables

Table 4.1. Model parameters.

Parameter	Explanation
β_0	The proportion of study individuals that were potentially observable during the first survey. Study individuals exclude those that died prior to the first survey and those beneath the minimum observable size for the entire study period. Potentially observable individuals include those that were not observed due to oversight.
$\theta_{S,0}$ $\theta_{S,1}$	Intercept and coefficient, respectively, of the log-linked linear function describing the spatially-averaged sitewide seed arrival rate as a function of the survey-specific sitewide seed release index.
α_D	Shape parameter of the gamma-distributed prior for the transect-specific dispersal factors. The prior is defined to have a mean of 1.
$\theta_{w,1}$	Coefficient describing the increase in the germination and initial establishment rate as a function of the relative duration a soil moisture category could not be assessed.
$\theta_{w,2}$	Coefficient describing the increase in the germination and initial establishment rate as a function of the relative duration a plot was underwater.
$\theta_{w,3}$	Coefficient describing the increase in the germination and initial establishment rate as a function of the relative duration a plot had a moist surface.
$\theta_{w,4}$	Coefficient describing the increase in the germination and initial establishment rate as a function of the relative duration a plot had a dry surface.
ϕ_{2010}	Daily survivorship rate from October 2009 to October 2010.
ϕ_{2011}	Daily survivorship rate from October 2010 to November 2011.
$\theta_{\phi,0}$	Intercept of the logit-linked linear function describing the survivorship rate from October 2009 to October 2010 as a function of one of four measured covariates.
$\theta_{\phi,1}$	Coefficient describing the increase in the survivorship rate as a function of the shear stress during peak flows.
$\theta_{\phi,2}$	Coefficient describing the increase in the survivorship rate as a function of the maximal depth to groundwater.
$\theta_{\phi,3}$	Coefficient describing the increase in the survivorship rate as a function of the average stressful groundwater elevation change rate.
$\theta_{\phi,4}$	Coefficient describing the increase in the survivorship rate as a function of the light index.
$p_{0,1}$	Probability a live stem was missed.
$p_{1,1}$	Probability a live stem was observed as alive.
$p_{2,1}$	Probability a live stem was observed as probably alive.
$p_{3,1}$	Probability a live stem was observed as probably dead.
$p_{4,1}$	Probability a live stem was observed as dead.
$p_{0,-1}$	Probability a dead stem was missed.
$p_{1,-1}$	Probability a dead stem was observed as alive. Assumed to be 0 due to observation criteria.
$p_{2,-1}$	Probability a dead stem was observed as probably alive.
$p_{3,-1}$	Probability a dead stem was observed as probably dead.
$p_{4,-1}$	Probability a dead stem was observed as dead.
$q_{v_1^+} - q_{v_{31}^+}$	Probability a stem was surveyed with a particular survey history. See Supporting Information for the full enumeration.

Table 4.2. Counts of individuals ever observed, mean per transect, and standard errors.

<i>Species</i> Location	All Individuals		Small Non-seedlings		Seedlings	
	Total	Mean (SE) indiv./trans.	Total	Mean (SE) indiv./trans.	Total	Mean (SE) indiv./trans.
<i>Populus fremontii</i>	45	0.76 (0.19)	25	0.42 (0.15)	5	0.08 (0.04)
Point bar	4	0.24 (0.11)	0	0.00 (0.00)	2	0.12 (0.08)
Cut bank	14	1.00 (0.43)	9	0.64 (0.31)	2	0.14 (0.10)
Riffle bank	27	0.96 (0.31)	16	0.57 (0.27)	1	0.04 (0.04)
<i>Salix exigua</i>	34	0.58 (0.32)	3	0.05 (0.05)	2	0.03 (0.02)
Point bar	33	1.94 (1.07)	3	0.18 (0.18)	2	0.12 (0.08)
Cut bank	1	0.07 (0.07)	0	0.00 (0.00)	0	0.00 (0.00)
Riffle bank	0	0.00 (0.00)	0	0.00 (0.00)	0	0.00 (0.00)
<i>Salix gooddingii</i>	100	1.69 (0.41)	47	0.80 (0.31)	23	0.39 (0.14)
Point bar	20	1.18 (0.47)	5	0.29 (0.19)	7	0.41 (0.35)
Cut bank	12	0.86 (0.39)	5	0.36 (0.29)	0	0.00 (0.00)
Riffle bank	68	2.43 (0.77)	37	1.32 (0.62)	16	0.57 (0.21)

Table 4.3. Summary statistics (minimum, first quartile, median, mean, third quartile, and maximum) of the survivorship covariates (shear stress, maximal groundwater depth, average stressful groundwater elevation change rate, and illuminance relative to full sunlight).

Covariate Plots, period	Min	1st Q	Median	Mean	3rd Q	Max
Shear stress (Pa)						
All plots, spring 2010	0.00	0.00	0.00	1.35	0.00	25.19
All plots, summer 2010	0.00	0.00	0.00	2.38	0.00	32.15
Inundated plots, spring 2010	0.05	2.46	6.19	7.29	11.08	25.19
Inundated plots, summer 2010	0.00	3.58	8.38	9.89	15.51	32.15
Groundwater depth (m)						
All plots, spring 2010	0.00	1.25	1.86	1.83	2.36	6.76
All plots, summer 2010	0.00	1.38	2.04	2.23	2.82	9.88
Inundated plots, spring 2010	0.00	0.25	0.51	0.50	0.73	1.57
Inundated plots, summer 2010	0.00	0.52	0.80	0.80	1.09	1.97
Groundwater change (m/d)						
All plots, spring 2010	-0.0467	-0.0218	-0.0144	-0.0149	-0.0072	0.0000
All plots, summer 2010	-0.0724	-0.0164	-0.0105	-0.0130	-0.0055	0.0000
Inundated plots, spring 2010	-0.0409	-0.0200	-0.0099	-0.0114	-0.0016	0.0000
Inundated plots, summer 2010	-0.0276	-0.0112	-0.0083	-0.0085	-0.0056	0.0000
Relative illuminance						
All plots, spring 2010	0.01	0.44	0.64	0.61	0.81	1.02
All plots, summer 2010	0.00	0.42	0.64	0.61	0.83	1.02
Inundated plots, spring 2010	0.01	0.24	0.37	0.39	0.53	0.93
Inundated plots, summer 2010	0.00	0.19	0.36	0.37	0.52	1.01

Figures

Figure 4.1. Conceptual model of the recruitment process as a sequence of environmental filters on dispersed seeds. Initial establishment and recruitment are driven by seed production and release and can potentially occur only at sites that receive dispersed propagules, have a moist germination surface at the time of dispersal, are relatively free from light competition, have a sufficiently slow groundwater recession rate, have a suitably shallow groundwater table, and have little flood scour.

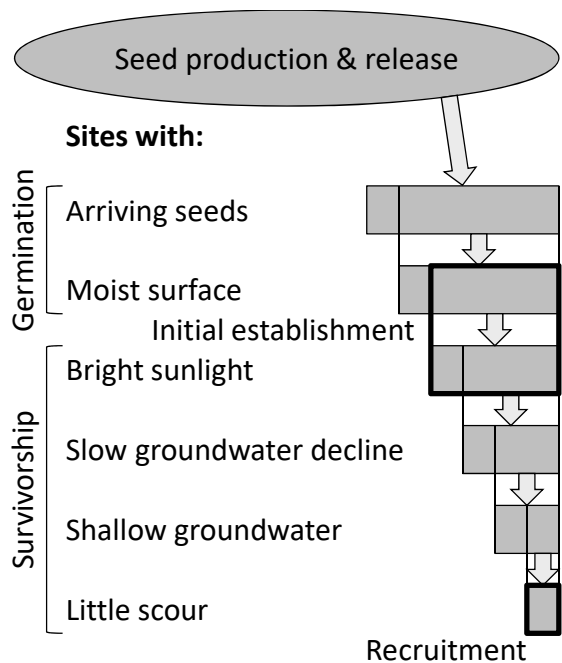


Figure 4.2. The location of the study site along the Merced River.

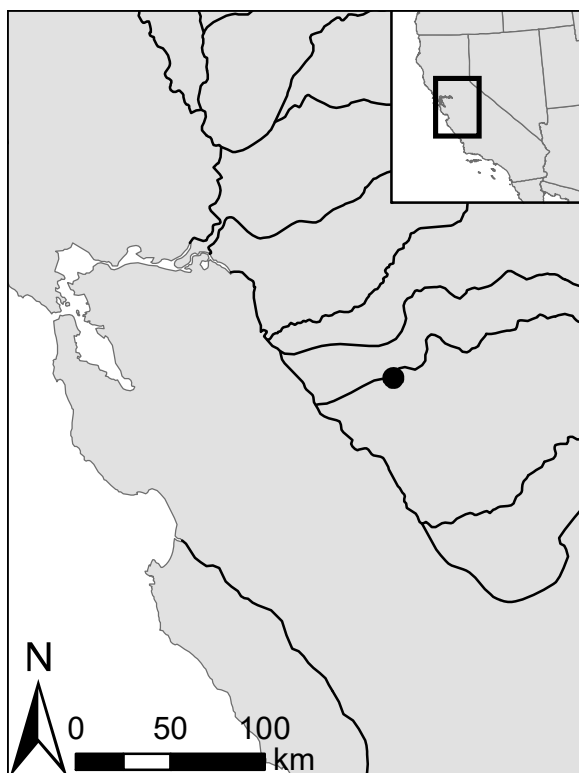


Figure 4.3. Merced River hydrograph at the Merced River near Snelling (MSN) gage located upstream of the Robinson Ranch (black line). Pre-dam flows at what is now New Exchequer Dam are underlain in light grey. The horizontal line marks the bankfull discharge. Survey dates are overlain.

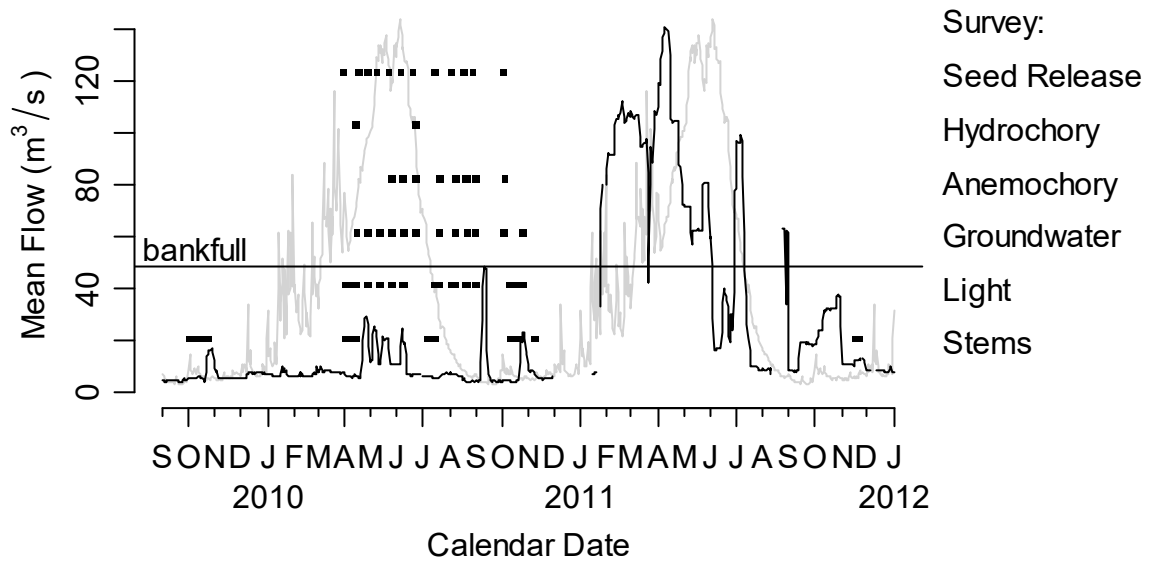


Figure 4.4. Temporal patterns of seed release and the arrival of viable seeds to the wind-dispersal seed traps. Seed release mean lines are bounded by one standard error. The viable seed supply horizontal error bars indicate the time period over which the sample was collected, and the vertical error bars denote one standard error. The viable seed supply lines merely connect measurements of the same species, and some dates are slightly offset for clarity.

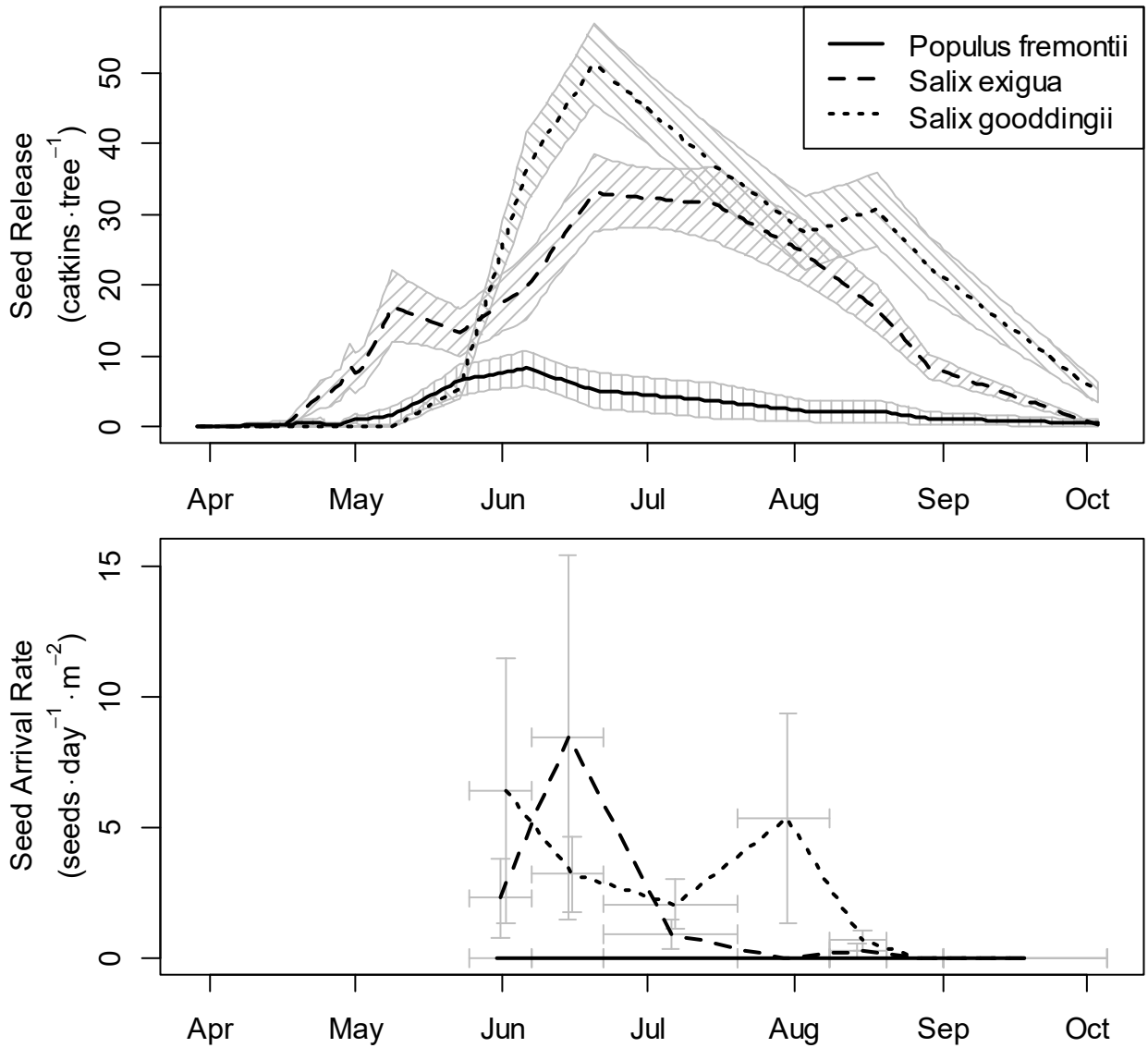


Figure 4.5. For each species, the arrival rates of viable seeds to the wind-dispersed seed traps at each transect, averaged over the sampled dispersal period. Points are horizontally jittered for visibility.

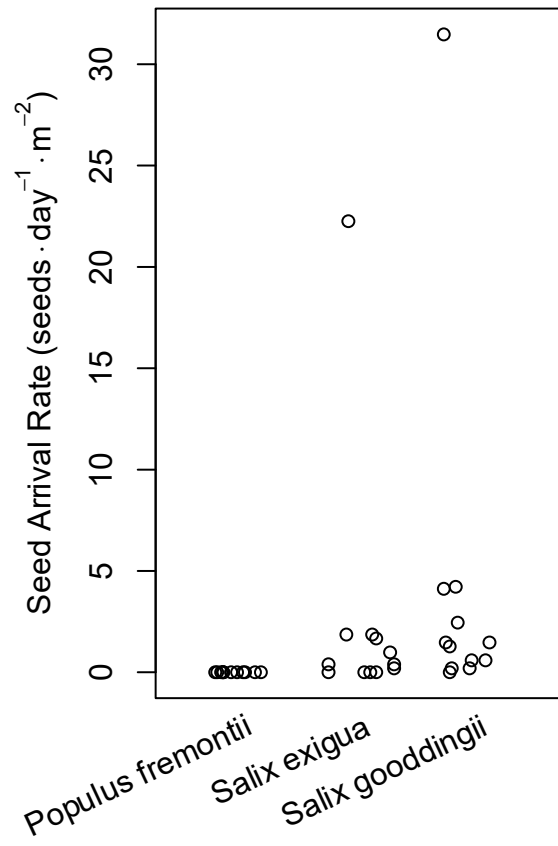


Figure 4.6. Boxplots summarizing the survivorship covariates (peak shear stress, maximal groundwater depth, average stressful groundwater elevation change rate, and illuminance relative to full sunlight) where individuals were observed. For example, the rightmost boxplot in the top right panel characterizes the peak shear stresses experienced by small non-seedling *Populus fremontii* individuals during the summer of 2010.

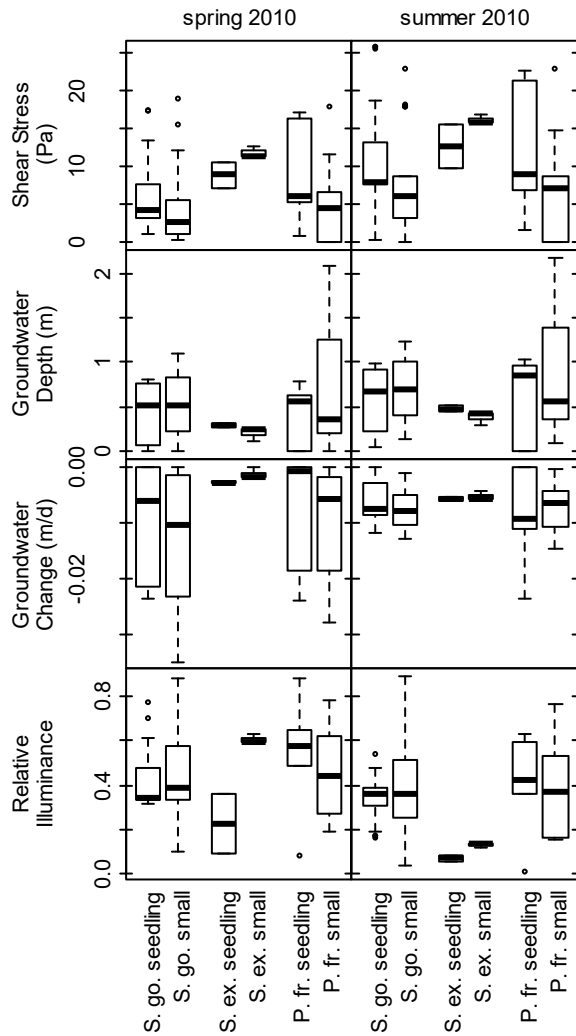


Figure 4.7. Posterior distributions for *Salix gooddingii* seedlings. The solid line marks the posterior mean, and the dashed lines denote inner 2.5% and 97.5% quantiles. Non-survey parameters are deferred to the Supporting Information.

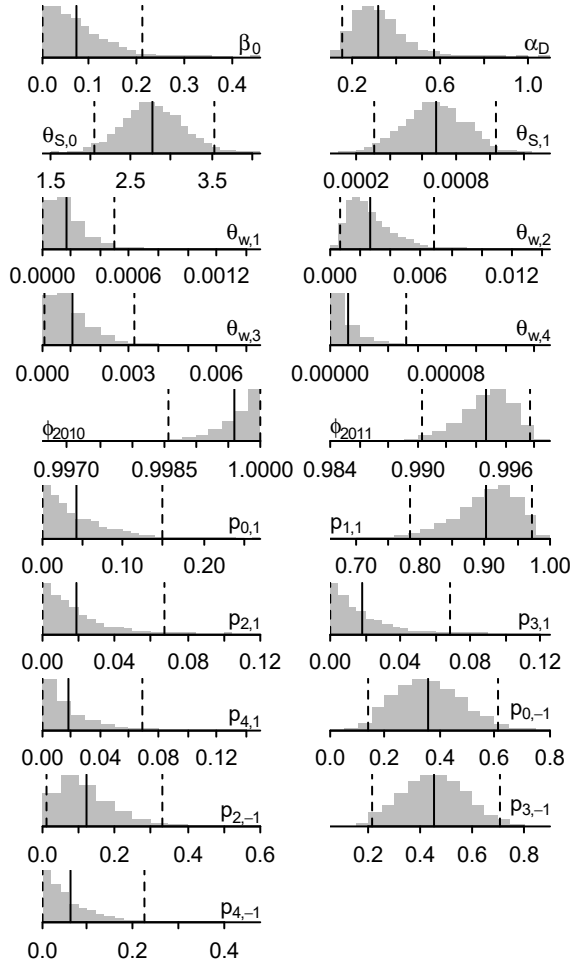


Figure 4.8. Posterior distributions for small *Salix gooddingii* individuals from the model in which survivorship is a function of the maximal depth to groundwater. The solid line marks the posterior mean, and the dashed lines denote inner 2.5% and 97.5% quantiles. Non-survey parameters are deferred to the Supporting Information.

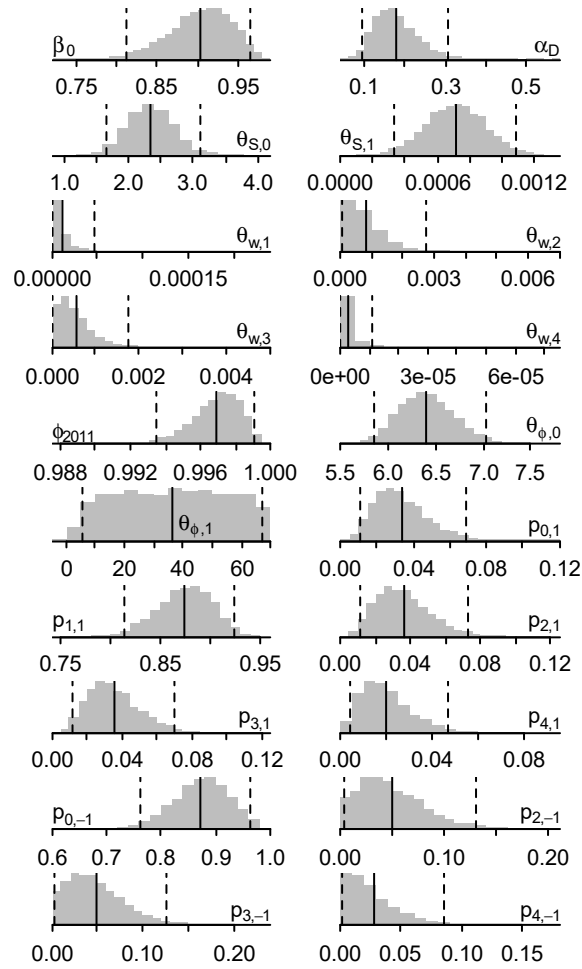
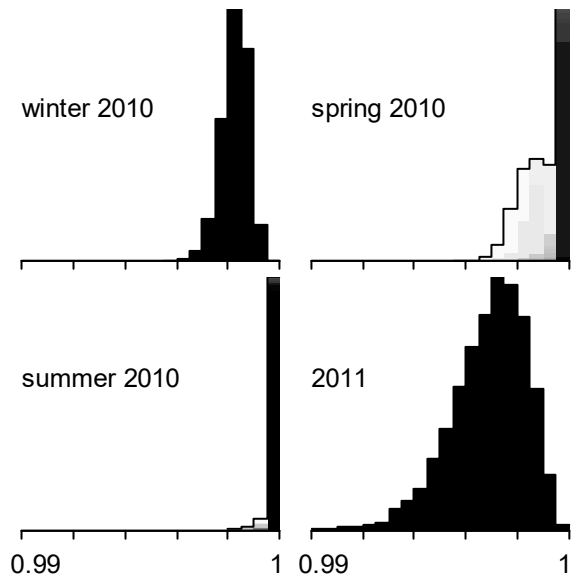


Figure 4.9. Posterior survivorship rates for small *Salix goodingii* individuals from the model in which survivorship is a function of the maximal depth to groundwater. When covariate data were available, individuals had different estimated survivorship rates, which are overlain with darker shading indicating greater agreement. The outermost edge of all of the overlain distributions combined is outlined for clarity.



Supporting Information

Model

The model used in this study simultaneously fits stem survey data, denoted by ω , and seed trap data, denoted by ζ . The stem survey model was based upon the hidden process capture-recapture model presented in Chapter III, and the notation described here is consistent. In this model, an individual had not yet recruited (τ'_0) or was alive at some plot ρ ($\tau'_{1,\rho}$) or was dead in plot ρ ($\tau'_{-1,\rho}$). Stem observation histories were sometimes incomplete, most often because only half of the transects were surveyed in 2011, but on rare occasions due to errors in the field. Therefore, at a particular plot ρ , a stem might not have been surveyed ($\psi'_{5,\rho}$), but if it was, then it was either not found (ψ'_0) or found and classified as alive ($\psi'_{1,\rho}$), probably alive ($\psi'_{2,\rho}$), probably dead ($\psi'_{3,\rho}$), or dead ($\psi'_{4,\rho}$). Although the model was formally defined with states and observations that are plot-specific, it can be convenient to describe stems regardless of location. Therefore, regardless of plot, stems might have been alive (τ'_1) or dead (τ'_{-1}), and might similarly have been observed with corresponding ψ'_0 through ψ'_5 .

At its core, the stem survey portion of the model simply describes the rate at which observed individuals occurred:

$$\begin{aligned} P([y_{\omega,\psi^+}] | [P(\psi|\tau)], [P(\tau|c)], [R_c]) &= \prod_{\psi^+} \mathbb{P}(y_{\omega,\psi^+} | R_{\psi^+}) \\ R_{\psi^+} &= \sum_{\tau} R_{\tau,\psi^+} \\ R_{\tau,\psi} &= R_{\zeta(\tau)} P(\tau | \check{\zeta}(\tau)) P(\psi | \tau), \end{aligned}$$

where the stem survey data (ω) are distinguished from seed trap data (ζ). To do so, it distinguishes between the observation (capture) history of an individual, ψ , which comprises a sequence of ψ' observations, and its actual fate, τ , which comprises a sequence of τ' states. The model necessarily distinguishes an observation history in which an individual was actually observed, ψ^+ , from one in which an individual was never observed, ψ^- . Each individual is a member of some cohort c , which comprises all individuals that recruited into the same state at the same time, and the cohort associated with the fate τ is given by the function $\check{c}(\tau)$.

As in the example presented in Chapter III, each observation history is associated with a survey history, v^+ , describing the occasions on which a stem was surveyed. The observation process distinguishes the probability of a survey history, $P(\check{v}^+(\psi))$, from the probability of the regular observations, $P(\psi|\check{v}^+(\psi), \tau)$:

$$P(\psi|\tau) = P(\check{v}^+(\psi)) P(\psi|\check{v}^+(\psi), \tau).$$

The probability of the regular observations is equivalent to an HMM:

$$P(\psi|\check{v}^+(\psi), \tau) = \prod_{t_\omega} p_{\check{\psi}'(\psi, t_\omega), \check{\tau}'(\tau, t_\omega), t_\omega}$$

where $p_{\psi'_{5,\rho}, \tau', t_\omega} = 1$ and the $\{p_{\psi', \tau', t_\omega} | \tau', \psi' \notin \{\psi'_{5,\rho}\}, t_\omega\}$ form a conditional distribution.

Obviously, stems that do not exist cannot be observed, so $p_{\psi'_0, \tau'_0, t_\omega} = 1$ and $p_{\psi'_{i,\rho}, \tau'_0, t_\omega} = 0$.

Stems were assumed to be observed only where they occurred, or in other words, $\rho_1 \neq \rho_2 \Rightarrow$

$p_{\psi'_{i,\rho_1}, \tau'_{j,\rho_2}, t_\omega} = 0$. All surveys were conducted by the same observer, so when a stem was

surveyed, we assume that observability parameters are the same regardless of time or place,

or in other words, we assume that $p_{\psi'_0, \tau'_{j,\rho}, t_\omega} = p_{0,j}$ and that $p_{\psi'_{i,\rho}, \tau'_{j,\rho}, t_\omega} = p_{i,j}$. With this

simplifying assumption, $p_{i,j} = P(\psi'_i | \tau'_j, i \neq 5)$, and the set $\{p_{i,j} | j, i \neq 5\}$ defines a

conditional distribution describing the probability of a stem in state τ'_j that was surveyed being observed as ψ'_i . Criteria for declaring a stem alive were strict enough that truly dead stems were never misidentified as alive, such that $p_{1,-1} = P(\psi'_1 | \tau'_{-1}) = 0$. The probability of a survey history was assumed not to depend on location, and so stems are either surveyed (v'_1) or not (v'_0). The survey history $\check{v}^+(\psi)$ is therefore defined such that $\check{v}'(\check{v}^+(\psi), t_\omega) = v'_0$ iff $\check{\Psi}'(\psi, t_\omega) \in \{\psi'_{5,\rho}\}$, and conversely, $\check{v}'(\check{v}^+(\psi), t_\omega) = v'_1$ iff $\check{\Psi}'(\psi, t_\omega) \notin \{\psi'_{5,\rho}\}$. Otherwise, the probabilities of the survey histories were treated as separate parameters q_{v^+} , or in other words, $P(v^+) = q_{v^+}$.

After recruitment, stem state transitions were assumed to be Markovian:

$$P(\tau | c) = \prod_{t_\omega > \check{\tau}(\tau)} \phi_{\check{\tau}'(\tau, t_\omega), \check{\tau}'(\tau, t_\omega + 1), t_\omega}$$

where $\check{\tau}(\tau)$ is the survey before an individual recruits. Obviously, plants do not migrate, so $\rho_1 \neq \rho_2 \Rightarrow \phi_{\tau_i, \rho_1, \tau_j, \rho_2, t_\omega} = 0$, and the remaining transitions are survivorship, $\phi_{\tau_{1,\rho}, \tau_{1,\rho}, t_\omega}$, and mortality, $\phi_{\tau_{1,\rho}, \tau_{-1,\rho}, t_\omega} = 1 - \phi_{\tau_{1,\rho}, \tau_{1,\rho}, t_\omega}$. Survivorship modeling was based upon a daily rate because different transects may have been surveyed on different days, although all plots on a transect were surveyed on the same day:

$$\phi_{\tau_{1,\rho}, \tau_{1,\rho}, t_\omega} = (\phi_{d,\rho, t_\omega})^{d_{\rho, t_\omega}},$$

where $\phi_{\tau_{1,\rho}, \tau_{1,\rho}, t_\omega}$ is the survivorship rate at plot ρ during the interval from stem survey t_ω to $t_\omega + 1$, ϕ_{d,ρ, t_ω} is the corresponding daily survivorship rate, and d_{ρ, t_ω} is the number of intervening days. In the uniform daily survivorship rate model, all plots share the same daily survivorship rate, which varies by year, ϕ_{2010} and ϕ_{2011} :

$$\phi_{d,\rho, t_\omega} = \begin{cases} \phi_{2010} & t_\omega \neq 4 \\ \phi_{2011} & t_\omega = 4. \end{cases}$$

By contrast, in the univariate logistic regression survivorship models, the daily survivorship rate was treated similarly to logistic regression:

$$\text{logit}(\phi_{d,\rho,t_\omega}) = \text{logit}(\Phi(\vec{\theta}_\phi, \vec{x}_{\phi,\rho,t_\omega}, k)) = \theta_{\phi,0} + \theta_{\phi,k} x_{\phi,\rho,t_\omega,k},$$

where $k = 1$ indicates the shear stress during peak flows, $k = 2$ indicates the maximal depth to groundwater, $k = 3$ indicates the average stressful groundwater elevation change rate, and $k = 4$ indicates the estimated light level at the ground surface. For computation, all survivorship covariates were centered and scaled, but the reported parameter estimates have had the transformations reversed.

In this case, $R_{c_{\tau'},t_\omega}$, the recruitment rate for the cohort that recruited into state τ' at after stem survey t_ω was modeled in more detail. The proportion of individuals in a plot that recruited prior to the first survey was assumed to be constant across plots:

$$R_{c_{\tau'},\rho,0} = \frac{\beta_0}{1 - \beta_0} \cdot \sum_{t_\omega > 0} R_{c_{\tau'},\rho,t_\omega}.$$

Recruitment during the study, $R_{c_{\tau'},\rho,t_\omega}$, was modeled as the product of transect- and survey-specific seed arrival rates, b_{ω,T,t_ω} , and germination fractions, γ_{ρ,t_ω} , all adjusted for the 0.0625 m² plot size:

$$R_{c_{\tau'},\rho,t_\omega} = 0.0625 \cdot \gamma_{\rho,t_\omega} \cdot b_{\omega,\tilde{T}(\rho),t_\omega},$$

where $\tilde{T}(\rho)$ simply indicates which transect plot ρ is situated upon. The germination fraction was a simple linear function:

$$\gamma_{\rho,t_\omega} = \sum_k \theta_{w,k} x_{d',\rho,t_\omega,k}$$

where each $\theta_{w,k}$ is the germination fraction under the k th soil moisture category and where $x_{d',\rho,t_\omega,k}$ is the proportion of days in the interval between stem surveys t_ω and $t_\omega + 1$

during which the plot ρ was assigned to the k th soil moisture category. The soil moisture categories were dry ($k = 4$), moist ($k = 3$), inundated ($k = 2$), and unknown ($k = 1$). The transect- and survey-specific seed arrival rate, b_{ω,T,t_ω} , was treated as the product of the survey-specific but spatially-averaged sitewide seed arrival rate, D_{ω,T,t_ω} , and a transect-specific spatial dispersal factor, a_T :

$$b_{\omega,T,t_\omega} = D_{\omega,T,t_\omega} a_T.$$

Although the sitewide seed arrival rate was essentially identical for all transects, variations in survey dates meant the actual rate was only the same for those transects surveyed on the same dates. The spatial dispersal factors, a_T , were assumed to be distributed according to a gamma distribution with mean 1 and shape parameter α_D , which implies the rate parameter was also equal to α_D , or in other words, $a_T \sim \mathbb{G}(\alpha_D, \alpha_D)$. These gamma distributed dispersal factors allow for spatial variation in dispersal while preserving the same mean sitewide seed arrival rate. The sitewide seed arrival rate, D_{ω,T,t_ω} , was a log linked linear function of the survey-specific sitewide seed release index, S_{ω,T,t_ω} , with coefficients $\theta_{S,0}$ and $\theta_{S,1}$:

$$\log(D_{\omega,T,t_\omega}) = \theta_{S,0} + \theta_{S,1} S_{\omega,T,t_\omega}.$$

The wind-dispersal seed trap data were modeled as independent samples from a Poisson distribution:

$$\begin{aligned} P\left(\left[y_{\zeta,T,t_\zeta}\right] \mid \dots\right) &= \prod_T P\left(\left[y_{\zeta,T,t_\zeta}\right] \mid \dots\right) \\ &= \prod_T \prod_{t_\zeta} \mathbb{P}\left(y_{\zeta,T,t_\zeta} \mid R_{\zeta,T,t_\zeta}\right), \end{aligned}$$

where y_{ζ,T,s_ζ} is the number of individuals observed in the wind-dispersal seed trap on transect T during dispersal survey t_ζ and $R_{\zeta,T,t_\zeta} = 0.0730 \cdot b_{\zeta,T,t_\zeta}$ is the corresponding seed arrival rate adjusted for the 0.0730 m^2 seed trap receiving area. Because the dispersal surveys were conducted on different dates from the stem surveys, we use seed arrival rates, b_{ζ,T,t_ζ} , sitewide seed arrival rates, D_{ζ,T,t_ζ} , and sitewide seed release indices, S_{ζ,T,t_ζ} , that are calculated based upon the dispersal survey dates.

For computational purposes, we integrated over the spatial dispersal factors, a_T :

$$P\left([y_{\omega,\psi^+}], [y_{\zeta,T,t_\zeta}] \mid \dots\right) = \int P\left([y_{\omega,\psi^+}], [y_{\zeta,T,t_\zeta}] \mid [a_T], \dots\right) P([a_T]) d[a_T],$$

where $P([a_T]) = \prod_T P(a_T) = \prod_T \mathbb{G}(a_T \mid \alpha_D, \alpha_D)$ is the gamma prior on the a_T . This integral can be analytically solved. Because stems do not migrate and because stems were observed only where they occurred, $R_{\tau,\psi} = 0$ if more than one plot ρ is associated with both τ and ψ , or more formally:

$$\left\| \bigcup_{t_\omega} \check{\rho}(\tau, t_\omega) \cup \check{\rho}(\psi, t_\omega) \right\| > 1 \Rightarrow R_{\tau,\psi} = 0,$$

where $\check{\rho}(\tau, t_\omega)$ gives the plot associated with the state $\check{\tau}'(\tau, t_\omega)$ or \emptyset if there is none, and similarly for $\check{\rho}(\psi, t_\omega)$. As a result, each $R_{\psi^+} > 0$ involves an observation history ψ^+ and a set of fates that are all effectively associated with a single plot $\check{\rho}(\psi^+)$. Therefore, the stem survey portion of the model can be factored by transect:

$$\prod_{\psi^+} \mathbb{P}(y_{\omega,\psi^+} \mid R_{\psi^+}) = \prod_T \prod_{\psi^+ \in \Psi^+(T)} \mathbb{P}(y_{\omega,\psi^+} \mid R_{\psi^+}),$$

where $\check{\Psi}^+(T) = \{\psi^+ | \check{\tau}(\check{\rho}(\psi^+)) = T\}$. Because the stem survey and seed trap data were treated as conditionally independent, then, the entire integral over the spatial dispersal factors can be marginalized by transect:

$$\begin{aligned} & \mathbb{P}\left([y_{\omega,\psi^+}], [y_{\zeta,T,t_\zeta}] \mid \dots\right) \\ &= \prod_T \int \left(\prod_{\psi^+ \in \check{\Psi}^+(T)} \mathbb{P}(y_{\omega,\psi^+} | R_{\psi^+}) \right) \left(\prod_{t_\zeta} \mathbb{P}(y_{\zeta,T,t_\zeta} | R_{\zeta,T,t_\zeta}) \right) \mathbb{P}(a_T) da_T. \end{aligned}$$

Not all transects that were surveyed for stems had seed traps, but for notational simplicity and concision, let $y_{\omega,\psi^+} = 0$ and $R_{\psi^+} = 0$ in such circumstances. Similarly, not all transects with seed traps were included in the stem surveys analyzed, so let $y_{\zeta,T,t_\zeta} = 0$ and $R_{\zeta,T,t_\zeta} = 0$ in those circumstances. Furthermore, those ψ^+ for which $R_{\psi^+} = 0$ can be effectively ignored, and the spatial dispersal factor can be factored out of the remaining R_{ψ^+} :

$$\begin{aligned} \eta_{\psi^+} &= \frac{R_{\psi^+}}{a_{\check{\tau}(\check{\rho}(\psi^+))}} = \sum_{\tau} \eta_{\check{c}(\tau)} \mathbb{P}(\tau | \check{c}(\tau)) \mathbb{P}(\psi | \tau) \\ \eta_{c'_{\tau_{1,\rho},t_\omega}} &= \frac{R_{c'_{\tau_{1,\rho},t_\omega}}}{a_{\check{\tau}(\rho)}} = 0.0625 \cdot \gamma_{\rho,t_\omega} \cdot D_{\omega,\check{\tau}(\rho),t_\omega}. \end{aligned}$$

Additionally, a similar factoring can be done for R_{ζ,T,t_ζ} :

$$\eta_{\zeta,T,t_\zeta} = \frac{R_{\zeta,T,t_\zeta}}{\alpha_T} = 0.0730 \cdot D_{\zeta,T,t_\zeta}.$$

For concision, let $\Gamma'(\alpha, \beta)$ be the normalization coefficient of the gamma distribution:

$$\Gamma'(\alpha, \beta) = \frac{\beta^\alpha}{\Gamma(\alpha)}.$$

Because the gamma distribution is the conjugate prior to the Poisson distribution, the integrand can be greatly simplified:

$$\begin{aligned}
\mathbb{P}(y|\eta a) \cdot \mathbb{G}(a|\alpha, \beta) &= \frac{(\eta a)^y}{y!} e^{-\eta a} \cdot \Gamma'(\alpha, \beta) a^{\alpha-1} e^{-\beta a} \\
&= \frac{\eta^y}{y!} \cdot \Gamma'(\alpha, \beta) \cdot a^{(\alpha+y)-1} e^{-(\beta+\eta)a} \\
&= \frac{\eta^y}{y!} \cdot \frac{\Gamma'(\alpha, \beta)}{\Gamma'(\alpha + y, \beta + \eta)} \cdot \mathbb{G}(a|\alpha + y, \beta + \eta).
\end{aligned}$$

By repeatedly utilizing this simplification, each spatial dispersal factor can be integrated out of the model:

$$\begin{aligned}
&\int \left(\prod_{\psi^+ \in \tilde{\Psi}^+(T)} \mathbb{P}(y_{\omega, \psi^+} | R_{\psi^+}) \right) \left(\prod_{t_\zeta} \mathbb{P}(y_{\zeta, T, t_\zeta} | R_{\zeta, T, t_\zeta}) \right) P(a_T) da_T \\
&= \left(\prod_{\psi^+ \in \tilde{\Psi}^+(T)} \frac{(\eta_{\psi^+})^{y_{\omega, \psi^+}}}{y_{\omega, \psi^+}!} \right) \cdot \left(\prod_{t_\zeta} \frac{(\eta_{\zeta, T, t_\zeta})^{y_{\zeta, T, t_\zeta}}}{y_{\zeta, T, t_\zeta}!} \right) \cdot \frac{\Gamma'(\alpha_D, \alpha_D)}{\Gamma'(\alpha_{\Gamma', T}, \beta_{\Gamma', T})}
\end{aligned}$$

where $\alpha_{\Gamma', T} = \alpha_D + \sum_{\psi^+ \in \tilde{\Psi}^+(T)} y_{\omega, \psi^+} + \sum_{t_\zeta} y_{\zeta, T, t_\zeta}$ and $\beta_{\Gamma', T} = \alpha_D + \sum_{\psi^+ \in \tilde{\Psi}^+(T)} \eta_{\psi^+} + \sum_{t_\zeta} \eta_{\zeta, T, t_\zeta}$.

Putting this together, we analyzed the fully integrated model:

$$\begin{aligned}
&\mathbb{P}([y_{\omega, \psi^+}], [y_{\zeta, T, t_\zeta}] | \dots) \\
&= \left(\prod_{\psi^+} \frac{(\eta_{\psi^+})^{y_{\omega, \psi^+}}}{y_{\omega, \psi^+}!} \right) \cdot \left(\prod_{T, t_\zeta} \frac{(\eta_{\zeta, T, t_\zeta})^{y_{\zeta, T, t_\zeta}}}{y_{\zeta, T, t_\zeta}!} \right) \cdot \left(\prod_T \frac{\Gamma'(\alpha_D, \alpha_D)}{\Gamma'(\alpha_{\Gamma', T}, \beta_{\Gamma', T})} \right).
\end{aligned}$$

Model priors were chosen to be uninformative. The q_{v^+} were given a uniform Dirichlet prior, as were the $\{p_{i,j} | j, i \neq 5\}$ with the exception of $p_{1,-1}$, and the remaining parameters were given widely bounded uniform priors. The seed release intercept $\theta_{S,0}$ was bounded within the interval $(-25, 10)$, while the corresponding coefficient $\theta_{S,1}$ was bounded within $(-0.01, 0.01)$. The parameter α_D , which defines the gamma prior for the spatial dispersal

factors, was similarly constrained to be positive and within the interval (0,100).

Survivorship coefficients, $\theta_{\phi,0}$ through $\theta_{\phi,5}$, were similarly widely bounded within (-100,100). The remaining parameters, β_0 , ϕ_{2010} , ϕ_{2011} , and $\theta_{w,1}$ through $\theta_{w,4}$, were bounded within (0,1).

Channel Cross-section Groundwater Geometry

The recruitment box model (Mahoney & Rood 1998) assumes the groundwater table near the river channel can be well approximated as horizontal. However, in some cases, the groundwater table can have a meaningful slope (Figure 4.S7). Given the slope of the river bank, θ , the size of the zone of capillary wetting, z , can be estimated as a function of the slope of the groundwater table, ϕ :

$$x = \frac{h_{\theta}}{\tan(\theta)} = \frac{h_{\phi}}{\tan(\phi)} = \frac{h - h_{\theta}}{\tan(\phi)}$$

$$h_{\theta} = \frac{h \cdot \tan(\theta)}{\tan(\theta) + \tan(\phi)}$$

$$z = \frac{h_{\theta}}{\sin(\theta)} = \frac{h}{\sin(\theta) + \cos(\theta) \cdot \tan(\phi)},$$

where h is the capillary fringe height and h_{θ} and h_{ϕ} partition h into above river surface and below river surface portions. The proportional error in the size of the zone of capillary wetting introduced by assuming a horizontal groundwater table can be quantified:

$$\frac{z_0}{z} = \frac{h}{\sin(\theta)} \cdot \frac{\sin(\theta) + \cos(\theta) \cdot \tan(\phi)}{h} = 1 + \frac{\tan(\phi)}{\tan(\theta)},$$

where z_0 is the size of the zone of capillary wetting assuming a horizontal groundwater table. For example, with a 10° bank slope and 5° declining groundwater table, assuming a horizontal groundwater table leads to a 50% overestimate of the size of the zone of capillary

wetting. Although a losing river is presented here, these relations can be applied to gaining rivers using a negative groundwater table slope, ϕ , with natural constraints such as the groundwater table being below the river bank.

Errors in the capillary fringe height can be similarly assessed. An erroneous capillary fringe height, $h + \Delta h$, leads to error in the size of the zone of capillary wetting:

$$\frac{z^+}{z} = 1 + \frac{\Delta h}{h}.$$

Although superficially representing an overestimated capillary fringe height, underestimates can be represented with negative Δh , again with natural constraints. For example, if the capillary fringe height were 30 cm, but were overestimated to be 50 cm, then the size of the zone of capillary wetting would be overestimated by 67%.

Small individual ages

In September 2011, ten *Salix gooddingii* and ten *Populus fremontii* individuals between 0.5–1 m in height were collected from the areas between the transects in order to estimate the ages of the larger and presumably older of the small individuals. There were too few non-clonal *Salix exigua* of this size to collect. Stems were sectioned at the root/stem interface, sanded, and rings counted. For both species, the average age was 5.6 years, ranging from 4–9 years for *Populus fremontii* and 4–8 years for *Salix gooddingii*. However, these estimated ages are inherently imprecise. Both species have semi-diffuse wood, which makes it difficult to distinguish narrow rings. Furthermore, both species can resprout, rendering ring counts underestimates. Finally, seedlings of these species are especially sensitive to soil moisture, which can potentially lead to both missing and false rings,

depending on precipitation, flooding, and stem position. Therefore, we only interpret these data as suggesting the small individuals were older than 2–3 years.

Populus fremontii dispersal period

There is some disagreement over the dispersal period for *Populus fremontii*. We observed seed release at a single site for one year, and dispersal occurred from May to August. Stella (2005) observed seed release at 6 sites over 3 years, and dispersal occurred anywhere from April to August, typically for around 3 months at any particular site in any particular year. Although we observed seed arrival, no *Populus fremontii* was observed. Fenner et al. (1985) measured seed arrival at a single site for one year, and dispersal occurred for roughly 1.5 months in April and May. Warren and Turner (1975) measured *Populus fremontii* seed arrival at a single site for one year, and dispersal also occurred for roughly 1.5 months in April and May. The discrepancy between seed arrival measured in seed traps and seed release measured through catkin counts is likely due in part to local adaptations to regional differences between Mediterranean climate California and arid Arizona and due in part to older open catkins that are largely depleted of seeds but are indistinguishable from younger actively releasing catkins. Finally, Braatne et al. (1996) reported that *Populus fremontii* dispersed seeds in March and April, noticeably earlier than all other studies, citing Reichenbacher (1984). However, Reichenbacher (1984) did not study or report any dispersal period for *Populus fremontii*. By contrast, Wyckoff & Zasada (2008), in an update to Schreiner (1974), report a March and April dispersal period for *Populus fremontii* from Arizona. Nonetheless, there is some indication that *Populus fremontii* populations in warmer regions may begin to disperse seeds earlier than populations in cooler regions.

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Supporting Tables

Table 4.S1. Model survey history parameters enumerated. At each survey occasion, a stem is either surveyed (v'_1) or not (v'_0).

parameter	explanation
$q_{v_1^+}$	Probability a stem was surveyed with survey history $v'_0 v'_0 v'_0 v'_0 v'_1$.
$q_{v_2^+}$	Probability a stem was surveyed with survey history $v'_0 v'_0 v'_0 v'_1 v'_0$.
$q_{v_3^+}$	Probability a stem was surveyed with survey history $v'_0 v'_0 v'_0 v'_1 v'_1$.
$q_{v_4^+}$	Probability a stem was surveyed with survey history $v'_0 v'_0 v'_1 v'_0 v'_0$.
$q_{v_5^+}$	Probability a stem was surveyed with survey history $v'_0 v'_0 v'_1 v'_0 v'_1$.
$q_{v_6^+}$	Probability a stem was surveyed with survey history $v'_0 v'_0 v'_1 v'_1 v'_0$.
$q_{v_7^+}$	Probability a stem was surveyed with survey history $v'_0 v'_0 v'_1 v'_1 v'_1$.
$q_{v_8^+}$	Probability a stem was surveyed with survey history $v'_0 v'_1 v'_0 v'_0 v'_0$.
$q_{v_9^+}$	Probability a stem was surveyed with survey history $v'_0 v'_1 v'_0 v'_0 v'_1$.
$q_{v_{10}^+}$	Probability a stem was surveyed with survey history $v'_0 v'_1 v'_0 v'_1 v'_0$.
$q_{v_{11}^+}$	Probability a stem was surveyed with survey history $v'_0 v'_1 v'_0 v'_1 v'_1$.
$q_{v_{12}^+}$	Probability a stem was surveyed with survey history $v'_0 v'_1 v'_1 v'_0 v'_0$.
$q_{v_{13}^+}$	Probability a stem was surveyed with survey history $v'_0 v'_1 v'_1 v'_0 v'_1$.
$q_{v_{14}^+}$	Probability a stem was surveyed with survey history $v'_0 v'_1 v'_1 v'_1 v'_0$.
$q_{v_{15}^+}$	Probability a stem was surveyed with survey history $v'_0 v'_1 v'_1 v'_1 v'_1$.
$q_{v_{16}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_0 v'_0 v'_0 v'_0$.
$q_{v_{17}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_0 v'_0 v'_0 v'_1$.
$q_{v_{18}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_0 v'_0 v'_1 v'_0$.
$q_{v_{19}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_0 v'_0 v'_1 v'_1$.
$q_{v_{20}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_0 v'_1 v'_0 v'_0$.
$q_{v_{21}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_0 v'_1 v'_0 v'_1$.
$q_{v_{22}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_0 v'_1 v'_1 v'_0$.
$q_{v_{23}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_0 v'_1 v'_1 v'_1$.
$q_{v_{24}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_1 v'_0 v'_0 v'_0$.
$q_{v_{25}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_1 v'_0 v'_0 v'_1$.
$q_{v_{26}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_1 v'_0 v'_1 v'_0$.
$q_{v_{27}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_1 v'_0 v'_1 v'_1$.
$q_{v_{28}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_1 v'_1 v'_0 v'_0$.
$q_{v_{29}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_1 v'_1 v'_0 v'_1$.
$q_{v_{30}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_1 v'_1 v'_1 v'_0$.
$q_{v_{31}^+}$	Probability a stem was surveyed with survey history $v'_1 v'_1 v'_1 v'_1 v'_1$.

Table 4.S2. Seed arrival fluxes. In all studies, traps collected seeds for multiple days between collections, so calculated fluxes are the average over the collection period. The peak mean flux is the peak over time of the mean flux across locations, with the standard error at the time of the peak given in parentheses where available. The mean daily flux, by contrast, is the mean rate over the entire dispersal period. For the current study, the annual flux was annualized from the mean daily flux based on the estimated dispersal period. For Gage & Cooper (2005), the fitted flux rate at 50 m from a seed source and the fitted asymptotic rate are shown, in that order, with the range of observed rates given in parentheses.

Source Detail	Peak mean flux (seeds·day⁻¹·m⁻²)	Mean daily flux (seeds·day⁻¹·m⁻²)	Annual flux (seeds·yr⁻¹·m⁻²)
Current study			
<i>Populus fremontii</i>	0 (±0)	0 (±0)	0 (±0)
<i>Salix exigua</i>	8.45 (±6.99)	2.46 (±1.82)	184 (±136)
<i>Salix gooddingii</i>	6.41 (±5.09)	3.99 (±2.53)	299 (±190)
Warren & Turner (1975)			
<i>Baccharis glutinosa</i>	40	27.5	2360
<i>Populus fremontii</i>	132	13.5	1340
<i>Tamarix chinensis</i>	1030	194	35600
Fenner et al. (1985)			
<i>Populus fremontii</i>	42	17	1000
Gage & Cooper (2005)			
<i>Salix</i> spp.			
Horseshoe Park	NA	3.38; 1.80 (0.984–114)	149; 79 (43–5020)
Moraine Park	NA	6.26; 0.474 (0.0229–176)	276; 21 (1–7780)

Table 4.S3. Germination rates derived from field studies. Cooper & Andersen (2012) studied *Populus fremontii* ssp. *fremontii* and *Populus deltoides* ssp. *wislizeni* together along with hybrids, without further distinguishing. Given values are the mean, the mean and standard error, or the range of means and range of 2.5% quantiles and range of 97.5% quantiles.

Source and detail	Germination rate
Current study	
<i>Salix gooddingii</i>	
Spring 2010	0.07–0.23% [(0.02–0.06%)–(0.18–0.59%)]
Summer 2010	0.02–0.23% [(0.01–0.07%)–(0.04–0.55%)]
Cooper et al. (1999)	
<i>Populus deltoides</i> ssp. <i>wislizenii</i>	
Deer Lodge Park, 1995 cohort	49.4%
Gage & Cooper (2005)	
<i>Salix</i> spp.	
Moraine Park, 50 m	0.5%
Moraine Park, asymptotic	1.2%
Cooper & Andersen (2012)	
“Fremont cottonwood”	
Lower Grimes, control treatments	0.37% (±0.19%)
Upper Grimes, control treatments	0.14% (±0.04%)
Sub-HQ, control treatments	0.19% (±0.07%)
Lower Hog, control treatments	1.29% (±0.39%)
Upper Hog, control treatments	2.25% (±1.54%)
Allen, no treatments	5.97%

Table 4.S4. Survivorship rates estimated in this study compared with survivorship rates measured in no-drawdown controls from other experimental studies. Shown survivorship rates are the mean, the mean and 2.5 and 97.5% quantiles, or the range of means and range of 2.5% quantiles and range of 97.5% quantiles.

Source and detail	Daily survivorship rate
Current study	
<i>Salix gooddingii</i>	
Seedlings	
2010	99.96% (99.86–100%)
2011	99.47% (99.03–99.77%)
Small individuals, groundwater depth model	
Winter 2010	99.83% (99.71–99.91%)
Spring 2010	99.83–100% [(99.71–100%)–(99.91–100%)]
Summer 2010	99.99–100% [(99.92–100%)–(100–100%)]
2011	99.69% (99.35–99.91%)
Mahoney & Rood (1991)	
<i>Populus deltoides</i> × <i>P. balsamifera</i> , 0 cm/d	99.7%
Amlin & Rood (2002)	
<i>Populus balsamifera</i> , 0 cm/d	99.4%
<i>Populus deltoides</i> , 0 cm/d	97.7%
<i>Salix exigua</i> , 0 cm/d	96.9%
<i>Salix lutea</i> , 0 cm/d	99.3%
Stella (2005)	
<i>Populus fremontii</i> , 0 cm/d	99.3%
<i>Salix exigua</i> , 0 cm/d	99.2%
<i>Salix gooddingii</i> , 0 cm/d	99.7%

Supporting Figures

Figure 4.S1. Posterior distributions for *Salix gooddingii* seedlings. The solid line marks the posterior mean, and the dashed lines denote inner 2.5% and 97.5% quantiles.

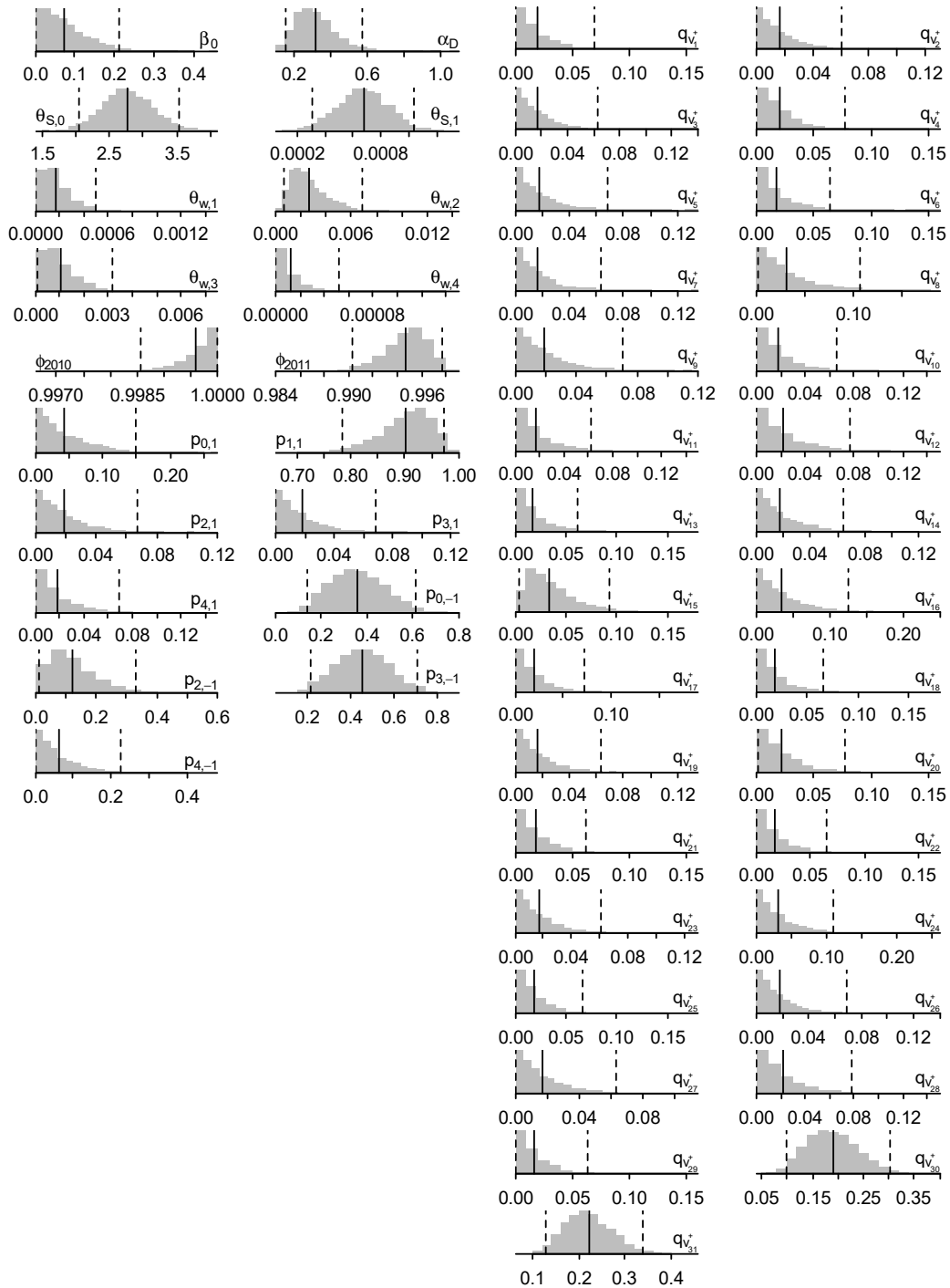


Figure 4.S2. Posterior distributions for small *Salix gooddingii* individuals from the model in which survivorship is a function of the peak shear stress. The solid line marks the posterior mean, and the dashed lines denote inner 2.5% and 97.5% quantiles.

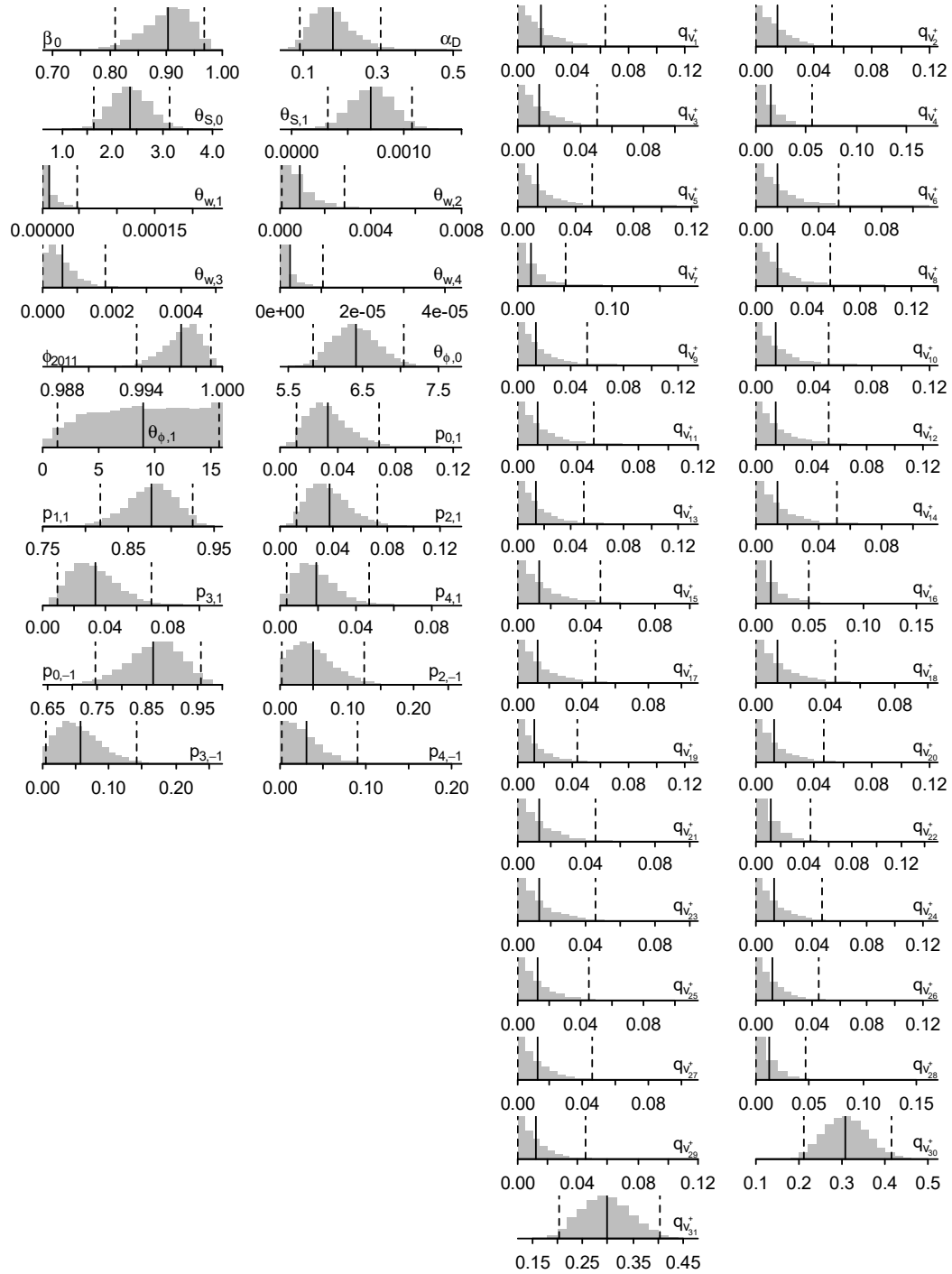


Figure 4.S3. Posterior distributions for small *Salix gooddingii* individuals from the model in which survivorship is a function of the maximal depth to groundwater. The solid line marks the posterior mean, and the dashed lines denote inner 2.5% and 97.5% quantiles.

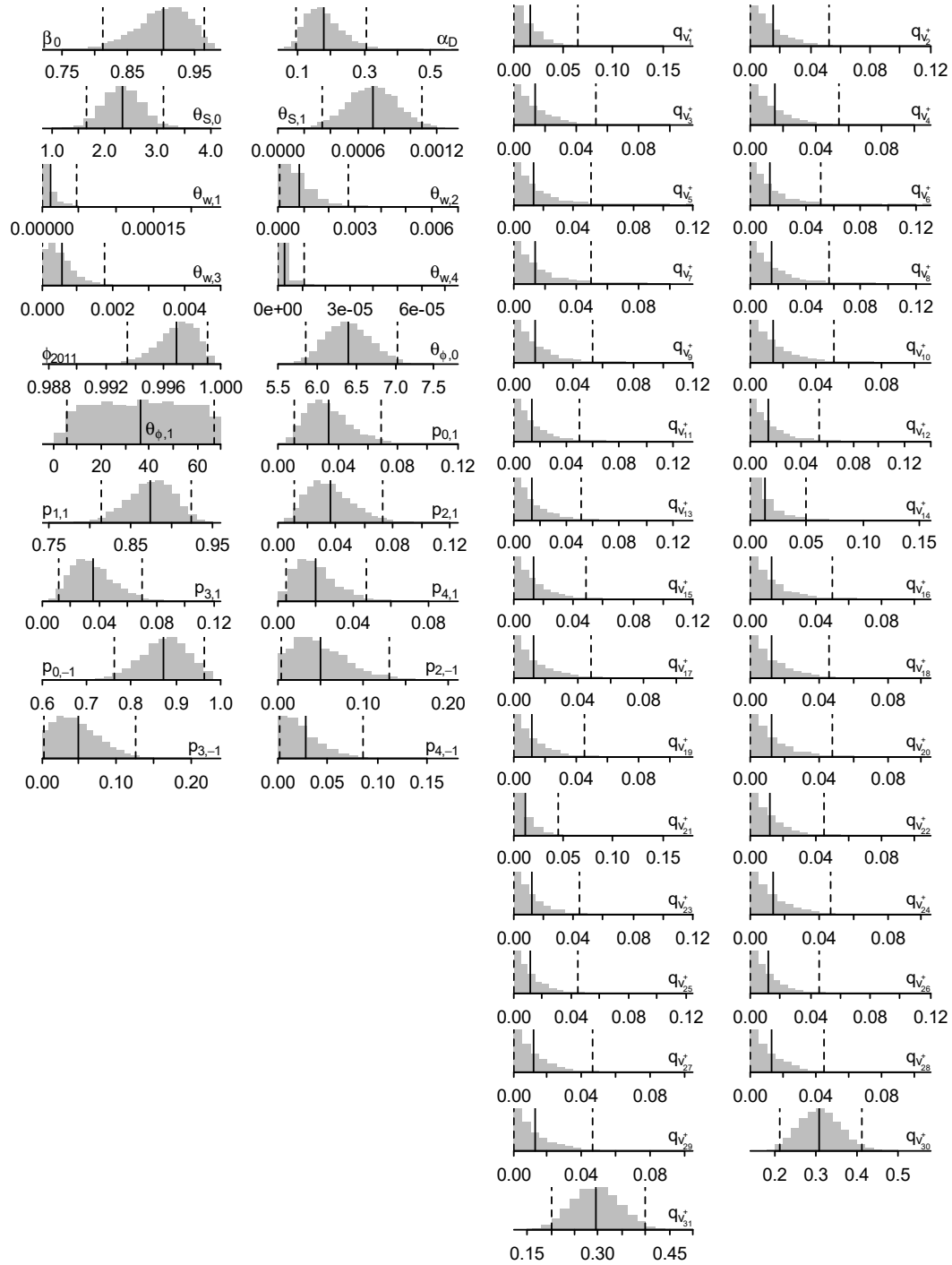


Figure 4.S4. Posterior distributions for small *Salix gooddingii* individuals from the model in which survivorship is a function of the average stressful groundwater elevation change rate. The solid line marks the posterior mean, and the dashed lines denote inner 2.5% and 97.5% quantiles.

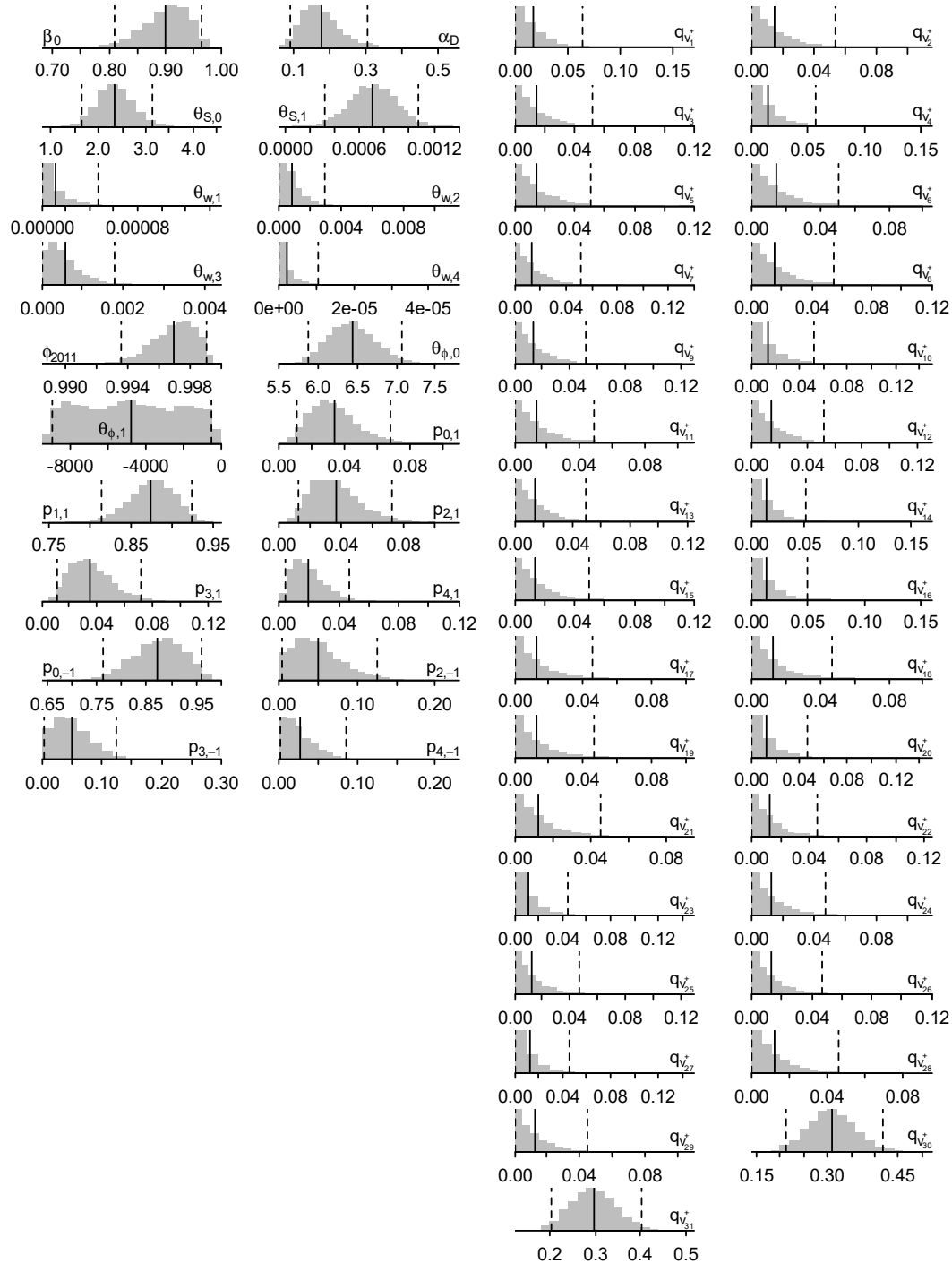


Figure 4.S5. Posterior distributions for small *Salix gooddingii* individuals from the model in which survivorship is a function of the illuminance index. The solid line marks the posterior mean, and the dashed lines denote inner 2.5% and 97.5% quantiles.

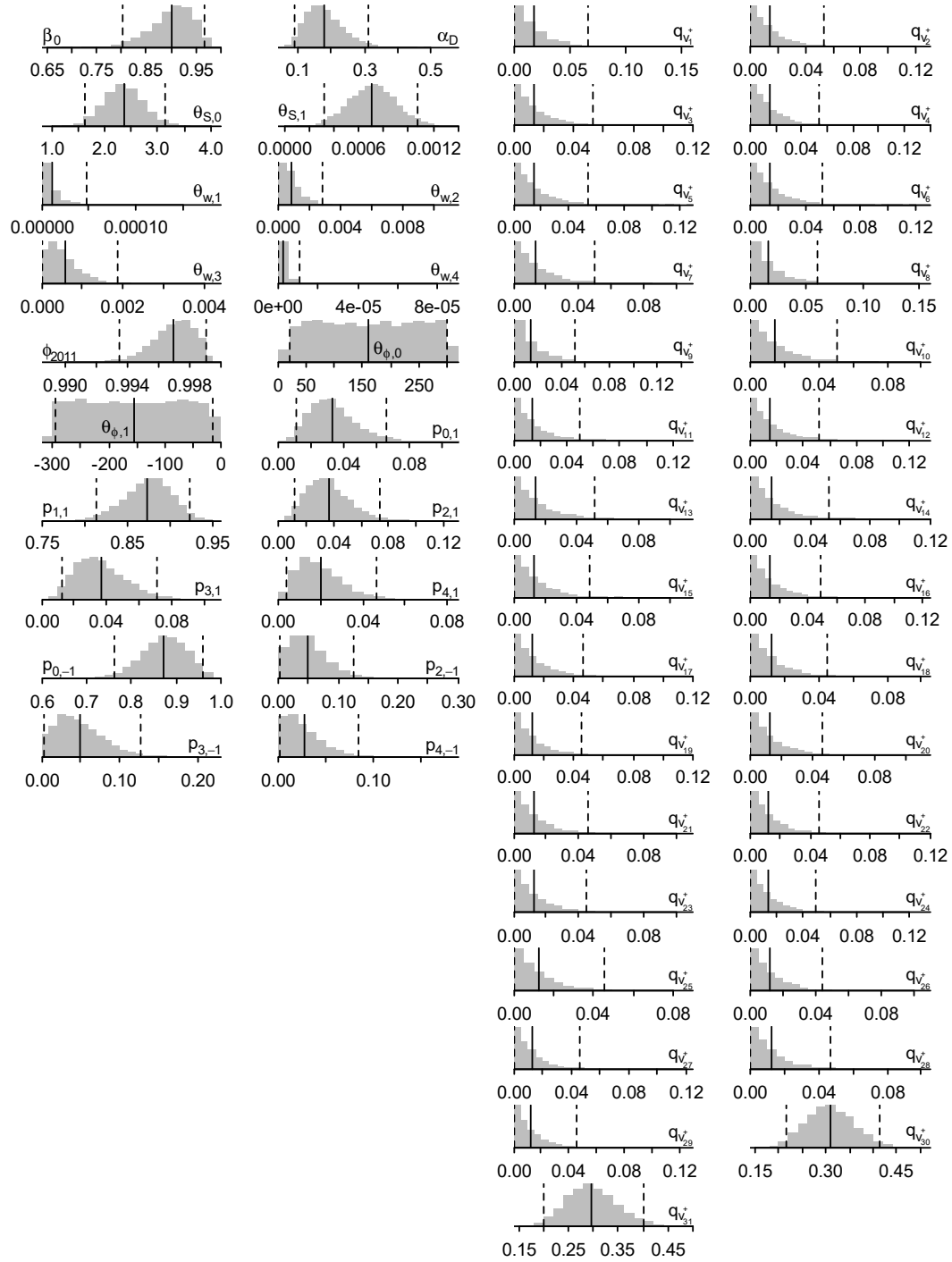


Figure 4.S6. Posterior survivorship rates for small *Salix goodingii* individuals from the model in which survivorship is a function of (a) the peak shear stress, (b) the maximal depth to groundwater, (c) the average stressful groundwater elevation change rate, and (d) the illuminance index. The posterior distributions for the individuals are overlain, with darker shading indicating greater agreement. The outermost edge of all of the distributions combined is outlined for clarity.

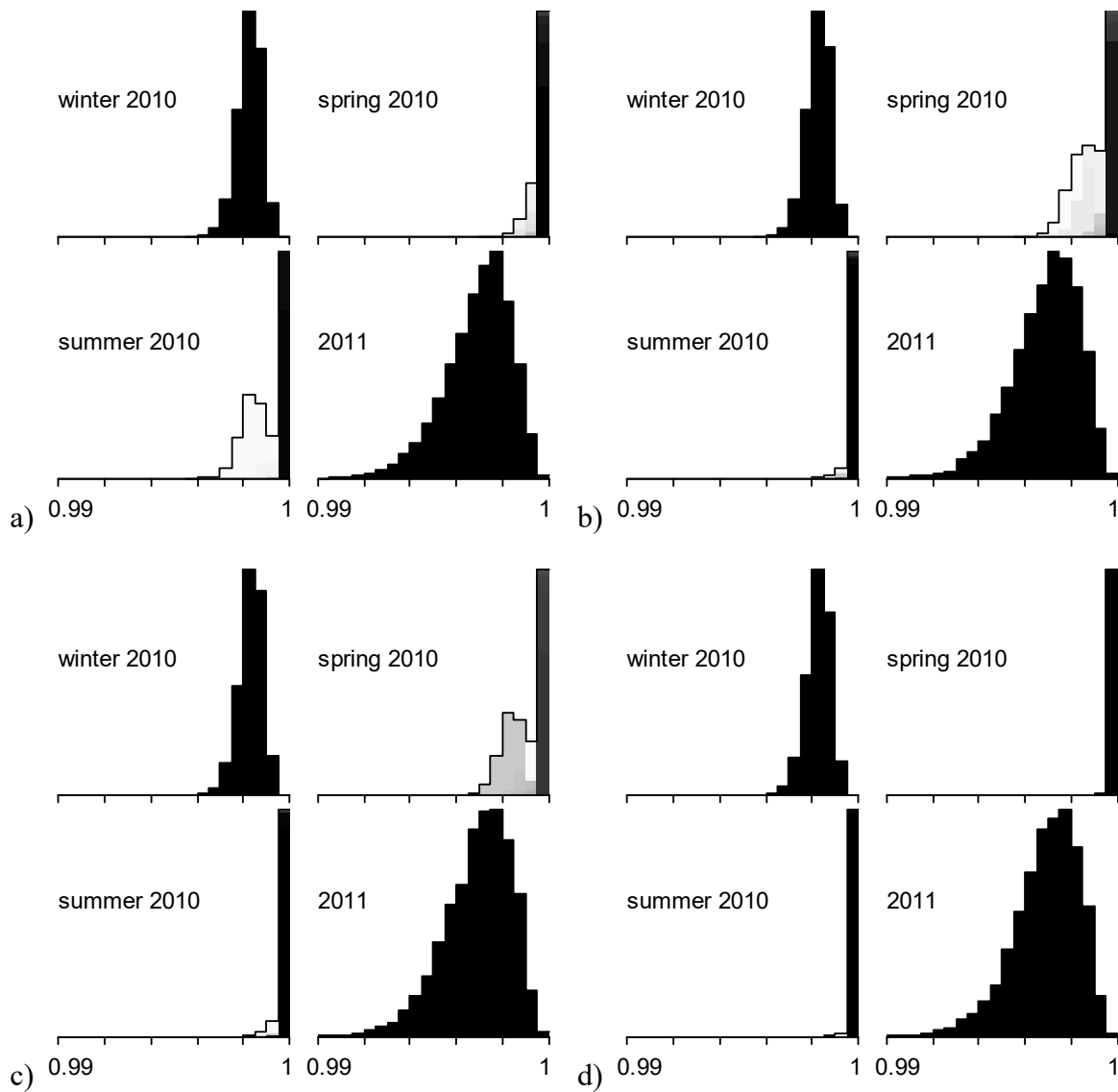


Figure 4.S7. Conceptual channel cross-section and groundwater table. The river bank (dashed line) has slope θ , the water table (dotted line) consists of the horizontal water surface within the channel and a groundwater table with slope ϕ . The capillary fringe height, h , determines the zone of capillary wetting, z . Although a losing river is shown, the diagram and geometry apply equally well to gaining rivers with negative slope ϕ .

