Canopy of the closed-cone pine forest dominated by mature bishop pine (*Pinus muricata*), just outside the perimeter of the 1995 Vision Fire on the north side of Inverness Ridge, Point Reyes National Seashore. All photographs by Brian J. Harvey.

FOREST RESILIENCE FOLLOWING SEVERE WILDFIRE IN A SEMI-URBAN NATIONAL PARK

by Brian J. Harvey, Barbara A. Holzman, and Alison B. Forrestel

When most of us think of forest fires, we likely invoke images of the 1988 fires in Yellowstone or the 2013 Rim Fire in Yosemite—wildfires in national parks or national forests far away from urban areas. Over the last half century, we've learned volumes about the importance of wildfires in these large, relatively remote expanses of forest. But what about forests that exist within a morning commute from places like San Francisco or Los Angeles? What role does fire play in the coastal conifer forests that neighbor some of the major cities in California?

CALIFORNIA CLOSED-CONE PINE FOREST

One such ecosystem is the closed-cone pine forest, which exists in a narrow band of disconnected populations along the Pacific Coast of California and Baja California. Many of these forests are dominated by bishop pine (*Pinus muricata*), a medium sized tree that typically lives to be 80–100 years old before succumbing to disease or pests. Bishop pines bear serotinous cones that remain sealed with resin until the heat of a fire breaks the cone scales open and releases seeds; therefore reproduction in the absence of fire is rare. Mature bishop pine trees are easily killed by fire, but the synchronous release of most seeds immediately following a fire allows for abundant post-fire seedling establishment. As such, most bishop pine forests are even-aged stands that originated after fire (Sugnet 1985).

One of the largest native bishop pine forests in the world exists in and around Point Reyes National Seashore, approximately 30 miles north of San Francisco. Until 1995, most forest stands in Point Reyes had not experienced fire in 60–80 years. Many mature bishop pine trees were approaching the end of their lifespan and very few seedlings existed in the forest understory. This all changed abruptly in early October 1995 when a wildfire ignited just outside the eastern park boundary on Mount Vision. Over the course of several days, the 5,000 hectare (ha) Vision Fire burned through Point Reyes Peninsula during a period of steady warm, dry winds blowing from the east, eventually reaching the Pacific Ocean just days later. In the bishop pine forest, the fire severity was so high that nearly all pre-fire vegetation was killed.

The Vision Fire was an important ecological disturbance in one of the most prized natural areas in the San Francisco Bay Area, and provided a unique opportunity to study the role of fire in coastal California ecosystems. Concern over how the ecosystems at Point Reyes would respond to a severe fire was high, although observations suggested that the bishop pine forest was teeming with plant life within months following the fire (Ornduff and Norris 1997; Ornduff 1998). Here, we synthesize the scientific findings from longer-term post-fire research, focusing on vegetation changes in the bishop pine forest that have occurred over nearly two decades since the fire. We highlight insights gained from several studies and identify key unknowns and priorities for future research. Much of the research we describe was supported by a Doc Burr Educational Grant from the California Native Plant Society and a small grant from the US National Park Service.

THE END AND BEGINNING OF A FOREST

The severity of the Vision Fire transformed mature forest stands (approximately 750 trees/ha) into a charred landscape with few traces of living vegetation within days after the fire, but bishop pine population dynamics after the fire demonstrated enormous post-fire resiliency (the capacity to recover following fire). Once the pre-fire trees were killed, post-fire bishop pine seedling germination and establishment became critical for forest persistence. Released from cones on burned mature trees, bishop pine seeds covered the blackened soil within weeks of the fire, and seedlings sprouted within months (Ornduff and Norris 1997). Shortly thereafter, anyone would be hard pressed to say that the forest stands were not on their way back. One year post-fire, Holzman and Folger (2005) recorded an average of 250,000 bishop pine seedlings/ha—greater than a 300-fold increase from the pre-fire tree density! As seedlings grew into larger saplings and then young trees, intense competition for resources resulted in post-fire tree density decreasing to an average of approximately 15,000 live bishop pine trees/ha by 14 years after the fire (Harvey and Holzman 2014). This process is referred to as "self-thinning," and is expected to continue as surviving individuals grow larger at the expense of neighboring plants.

Burned and weathered bishop pine cones from a mature tree killed by the 1995 Vision Fire remain attached to a fallen branch in a canopy gap filled by sticky monkeyflower (*Mimulus aurantiacus*) in 2009.

POST-FIRE SUCCESSION AND FOREST STAND DEVELOPMENT

Plant community dynamics after the Vision Fire demonstrated a pattern common to many fire-prone Mediterranean ecosystems; that is, plant species diversity was highest in the first years following fire. Two years after the fire, 34 different plant species were present (Holzman and Folger 2005), but by 14 years post-fire this number had decreased to 21 species (Harvey and Holzman 2014). The peak in plant diversity immediately following fire results from the myriad fire adaptations exhibited by the native plants in this forest. While bishop pines store their seeds high in the forest canopy, blue blossom ceanothus (*Ceanothus thyrsiflorus*) and several manzanita species (*Manzanita* spp.) store theirs in a soil seedbank where they are stimulated to germinate after fire. Less dominant tree species such as coast live oak (*Quercus agrifolia*) and California bay/California laurel (*Umbellularia californica*) can resprout from their root crowns or their stems after fire. Small statured plants such as yellow bush lupine (*Lupinus arboreus*) and annual herbs in the *Lotus* genus specialize in colonizing recently burned areas, where they gain an early competitive advantage by fixing nitrogen through a symbiotic relationship with bacteria in their roots.

The fact that species diversity is at its highest immediately following fire illustrates the importance of fire in maintaining plant community structure in bishop pine forests. All species that were recorded at any point during the first 14 years following the fire were present in the first two years, after which some early post-fire specialists were outcompeted and later disappeared. It is likely that some of these may reemerge when the next fire comes through. Some non-native species were also recorded in the early post-

Severe fire renews the bishop pine forest. ABOVE: **Bishop pine forest stand that did *not* burn in the 1995 Vision Fire. Trees are approximately 80 years old and illustrate moderately sparse stand density representative of the pre-fire forest. No tree seedlings are present in the forest understory, indicative of a long interval since the last fire.** OPPOSITE TOP: **Post-fire bishop pine forest stand in 2009 in an area where *all* pre-fire trees were killed in the 1995 Vision Fire. Abundant seedlings established immediately following the fire, leading to high, but variable post-fire stand density.**

fire years. Australian fireweed (*Erechtites minima*) was of particular concern, as this species can rapidly colonize burned areas and form a long-lived soil seedbank. Park managers and volunteers removed Australian fireweed in 1996 and very few plants were observed up to six years after the fire. It is not clear if there are any long-term effects from Australian fireweed on post-fire forest dynamics; however, seedbanks of this species may be present in the forest soils now, and long-term effects may not be evident until another fire occurs.

The Vision Fire also promoted diversity in forest structure (tree density, shrub cover, and plant species composition) across the burned landscape (Harvey and Holzman 2014). Pre-fire forest density (approximately 750 stems/ha) was fairly uniform across space, but different pathways of post-fire forest stand development were evident immediately after the fire and have persisted nearly two decades later. Some stands that had the highest initial post-fire bishop pine seedlings (in a few cases over 1,000,000 seedlings/ha) have since proceeded along a densely-forested "closed-canopy pathway" with low shrub cover and plant species diversity. Other stands with initially lower bishop pine seedling establishment (approximately 40,000 seedlings/ha) have since proceeded along an "open-canopy pathway" with sparse canopy trees, high shrub cover (mostly blue blossom ceanothus), and high plant species diversity. This diversity in vegetation structure generated by fire is important for wildlife habitat diversity for many animals.

FIRE AND FOREST EXPANSION

In addition to the abundant tree regeneration within the footprint of pre-fire bishop pine stands, fire served as a catalyst for forest expansion into new areas. The forest nearly doubled its extent after the fire, encroaching into pre-fire coastal grassland and coastal scrub. Before the fire, bishop pine stands were

restricted primarily to the high-elevation portions of Inverness Ridge; after the fire, they expanded all the way from the ridge top to the Pacific Ocean (Forrestel et al. 2011). Forest expansion occurred close to both pre-fire stands and around solitary pre-fire bishop pine trees that were at times over 500 meters from the edge of a pre-fire contiguous forest stand (Harvey et al. 2011). These solitary trees were killed by the fire, but the seeds released from their serotinous cones resulted in dense post-fire stands that are now greater than 1,000 stems/ha. Similar to the regenerating stands in areas that were forest prior to the fire, many of these expanded forest stands are interspersed with thickets of blue blossom ceanothus, which increased in extent by more than 4,000% across the burned landscape. Findings from Forrestel et al. (2011) and Harvey et al. (2011) illustrate the importance of pre-fire legacies—the location of pre-fire individual trees, forest stands, and soil seedbanks—in shaping post-fire vegetation patterns that may last decades or more.

KEY UNKNOWNS AND FUTURE RESEARCH PRIORITIES

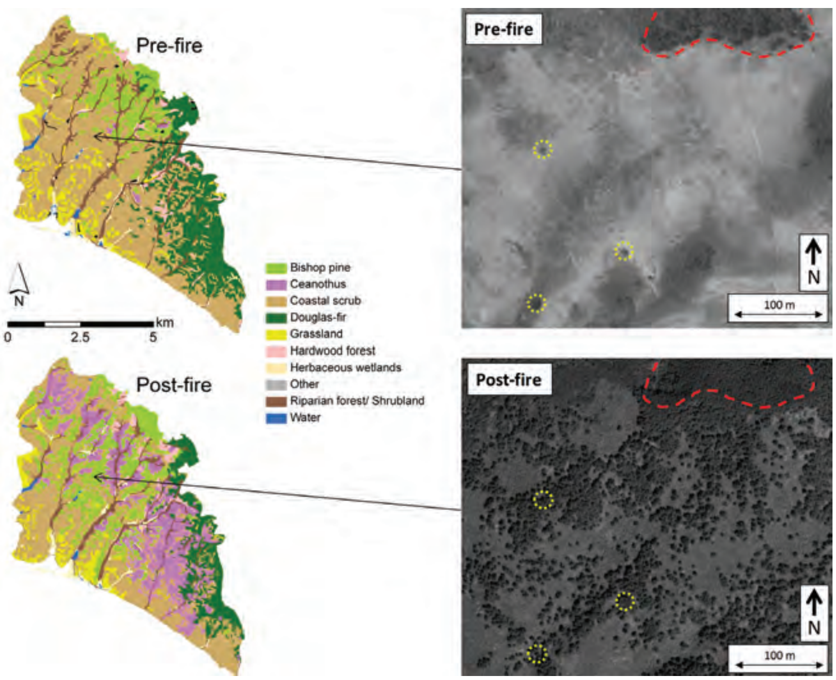
While the research following the 1995 Vision Fire provides insights into the disturbance ecology of coastal California pine forests, several key unknowns remain. First, mechanisms underpinning the patterns we observed over 14 post-fire years could be explored through careful experiments. Such designs could help determine the relative importance of initial seed influx (through soil or canopy seedbanks) compared to post-fire competitive interactions in determining the eventual landscape patterns of forest versus coastal scrub. Second, whether the evidence of forest resiliency and expansion following the Vision Fire is broadly representative of other populations of California closed-cone pines is unknown. Tracking post-fire trajectories or

Mature bishop pine cones on a 14-year-old tree that established after the 1995 Vision Fire. Bishop pine cones are strongly serotinous (they only open and release their seeds after being exposed to the heat of a fire), and are guarded from seed predators with spines on the tips of cone scales.

examining fire histories in other closed-cone pine forests could fill this knowledge gap. Third, with climate change likely to increase fire frequency, understanding the consequences of short-interval fires on the bishop pine forest is needed. If fires were to occur before the trees accumulate a sufficient aerial seedbank and shrubs and herbs accumulate a sufficient soil seedbank, post-fire resilience may be compromised. Finally, young post-fire bishop pine stands in Point Reyes have been recently impacted by pine pitch canker disease, leading to pockets of locally high tree mortality. Understanding the potential interactions between introduced disease and subsequent wildfire is another priority for future research.

The vegetation response following the Vision Fire illustrates the importance of wildfire in shaping one of the emblematic forest ecosystems in coastal California. Post-fire research spanning two decades at Point Reyes has demonstrated high natural resilience following severe wildfire in closed-cone pine forests—information that is critical to the conservation of this ecosystem. National Parks serve as vital scientific laboratories that provide insight into systems that extend beyond their borders. Parks such as Point Reyes National Seashore, which are within or close to urban areas, are especially unique as they offer an opportunity for visitors to understand the important processes that shape their local ecosystems.

FIGURE 1. BISHOP PINE FOREST EXPANSION CATALYZED BY FIRE.



LEFT: **Map of pre-fire (above) and post-fire (below) vegetation within the perimeter of the 1995 Vision Fire, illustrating the substantial change in spatial distribution of plant communities. In particular, the bishop pine forest (light green) expanded to the southwest.**

RIGHT: **Aerial photos taken in July 1993, two years before the Vision Fire (above), and August 2012, 17 years after the Vision Fire (below). Photos illustrate the dual modes of post-fire bishop pine forest expansion from pre-fire contiguous stands (dashed red line) and isolated pioneers (dotted yellow line). In both photos the lighter/non shadow-casting vegetation is grasses or shrubs whereas the darker/shadow-casting vegetation is bishop pine tree crowns.**

NOTE: **Black arrows connect the aerial photos to their corresponding location on the pre- and post-fire vegetation maps.**

SOURCE: **Maps are modified from Forrestel et al. (2011). Aerial photo data: Google, US Geological Survey, and DigitalGlobe.**

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