Arresting the spread of invasive species in continental systems

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Invasive species are a primary threat to biodiversity and are challenging to manage once populations become established in previously unoccupied areas. But removing them is further complicated when invasions occur in continental, mixed-ownership systems. We demonstrate a rare conservation success: the regional-scale removal of an invasive predator – the barred owl (*Strix varia*) – to benefit the spotted owl (*Strix occidentalis*) in California. Barred owl site occupancy declined sixfold, from 0.19 to 0.03, following 1 year of removals, and site extinction (0.92) far exceeded colonization (0.02). Spotted owls recolonized 56% of formerly occupied territories within 1 year, contrasting starkly with removals conducted after barred owls achieved high densities in the Pacific Northwest. Our study therefore averted the otherwise likely extirpation of California spotted owls (*Strix occidentalis occidentalis*) by barred owl competition. Collectively, leveraging technological advances in population monitoring, early intervention, targeting defensible biogeographic areas, and fostering public–private partnerships will reduce invasive species-driven extinction of native fauna in continental systems.

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Invasive species are a primary threat to biodiversity globally and can compromise ecosystem functions and services (Mack *et al*. 2000). Although most species extinctions resulting from biological invasions have occurred on islands, invasive species are becoming increasingly common and ecologically harmful in continental systems (Lodge *et al*. 2006). However, the establishment of invasive species frequently goes undetected on continents, allowing populations to grow rapidly and spread over large areas, which in turn makes subsequent management difficult or even intractable (Simberloff *et al*. 2005; Lodge *et al*. 2006). When expanding invasive species are allowed to become sufficiently abundant and widespread, management objectives often shift from range-wide eradication to more limited removals (1) within locally targeted areas to create refugia for native species or (2) at the leading edge of the invasion to contain further spread (Stewart-Koster *et al*. 2015).

Invasive species management that targets key ecological areas or the leading edge of an invasion in continental systems is challenged by the dispersal of individuals from source populations that provide continuous recruitment into managed areas (Phillips *et al*. 2006). Source populations are particularly likely to arise in mixed-ownership landscapes where incomplete landowner participation and public resistance to management constrain the ability to curb populations, resulting in a mosaic of low- and high-density areas (Epanchin-Niell *et al*. 2010). As a result, the relatively few compelling examples of successful management of invasive species in continental systems are often fueled by shared landowner and stakeholder support (Bryce *et al*. 2011), but are typically limited in geographic scale and fail to achieve complete eradication (Genovesi 2005; Robertson *et al*. 2017). What strategies, then, are likely to improve conservation outcomes when invasive species have already become widely distributed and achieved high densities in mixed-ownership landscapes, yet continue to expand across continental systems?

Here, we use the range expansion of the barred owl (*Strix varia*) into the Sierra Nevada (California) to illustrate and reinforce four approaches that can facilitate arresting the continental-scale expansion of an invasive apex predator at its invasion front. The barred owl has expanded from its native range in eastern North America into western forests over the past several decades, due most likely to anthropogenic landscape modifications, such as increases in forest cover in the Great Plains, but also potentially to natural processes (Dark *et al*. 1998; Livezey 2009). By virtue of their competitive dominance, barred owls pose an existential threat to the iconic and closely related northern spotted owl (*Strix occidentalis caurina*) in the Pacific Northwest (Kelly *et al*. 2003; Gutiérrez *et al*. 2007; Franklin *et al*. 2021). Furthermore, barred owls have a broad diet, consuming many ecologically important and sensitive prey species that are likely naïve to their hunting mode, and thus barred owls have the potential to substantially alter biological communities in western forests (Holm *et al*. 2016). Although the westward expansion of barred owls from their native range may be human-induced or a natural process,

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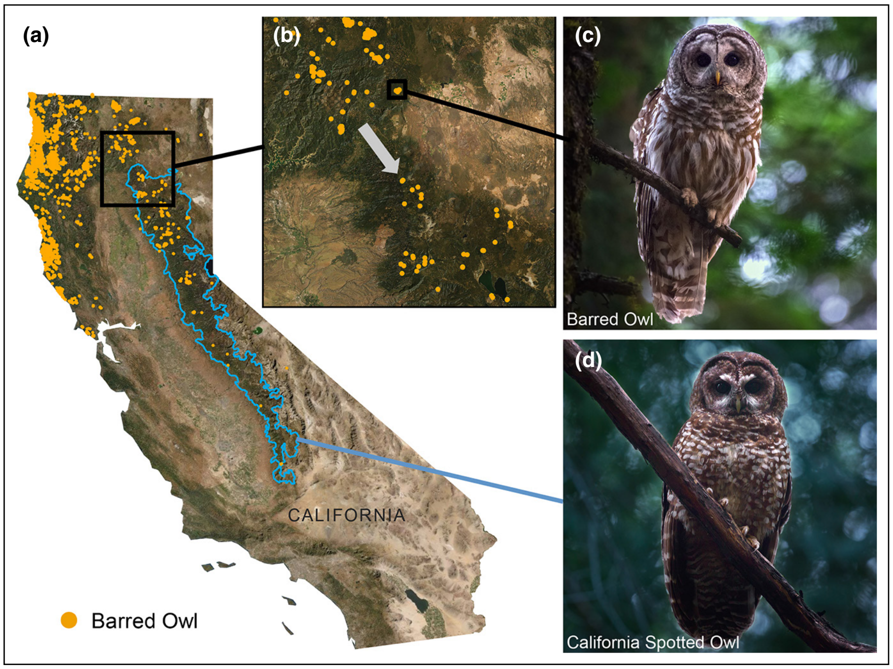

Figure 1. (a) Historical detections of barred owls and barred owl × spotted owl hybrids in California (California Department of Fish and Wildlife, https://wildlife.ca.gov/Data/CNDDB), depicted by orange dots overlaid on satellite imagery (source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, and IGN), showing the ecological similarity of the Sierra Nevada to an island. The range of the California spotted owl in the Sierra Nevada is depicted by the blue outline. (b) A narrow corridor (gray arrow) across the Pit River valley that is likely the main route that barred owls dispersing from the Klamath and Cascade ranges use to immigrate into the Sierra Nevada. (c and d) Images of a barred owl (*Strix varia*) and a California spotted owl (*Strix occidentalis occidentalis*), respectively.

precedent exists for managing gradually expanding species – including via lethal removal – when their ecological effects are sufficiently severe that they are considered invasive (Courchamp *et al*. 2003; Gese *et al*. 2015). Indeed, the US Fish and Wildlife Service has deemed the ecological impacts of barred owls on spotted owl populations and biological communities in western forests sufficient to both test the effectiveness of lethal removals and develop a long-term management plan for the species (FWS 2013). Small-scale experimental removals are ongoing at several locations in the Pacific Northwest where barred owls occur at very high densities and spotted owl populations have already declined substantially (Wiens *et al*. 2020). Because of a lag between initial invasion and management actions, however, recolonization by barred owls from unmanaged areas is rapid and recolonization by spotted owls is slow, requiring the removal of many individuals over multiple years to achieve even modest ecological benefits (Wiens *et al*. 2020).

In contrast, a multispecies passive acoustic monitoring (PAM) program revealed that barred owl density is relatively low in the Sierra Nevada, California, a presumed invasion front (Figure 1a; Wood *et al*. 2020). Yet the apparent initiation of rapid population growth in 2018 also indicated that barred owls in this region represent an imminent threat to another native spotted owl subspecies, the California spotted owl (*Strix occidentalis occidentalis*), as well as a suite of native species in this region of high biodiversity (Wood *et al*. 2021). The early detection of rapid barred owl population growth, coupled with shared conservation objectives among landowners and managers providing opportunities for decisive action, suggests that successful management may be more attainable in the Sierra Nevada than the Pacific Northwest. In addition, the Sierra Nevada is largely surrounded by non-forested habitat and thus functions as an island-like system likely connected to larger barred owl populations mainly via a narrow corridor at the northern end of the Sierra Nevada range – with these biogeographic barriers potentially limiting recolonization by barred owls (Figure 1b). We therefore hypothesized that a constellation of four elements can contribute to successfully arresting the expansion of invasive species in continental systems: (1) technological advances facilitating regional-scale surveillance and monitoring (eg PAM), (2) a decisive response in the early stage of expansion when invasive species density is low, (3) biogeographical barriers limiting colonization from source populations, and (4) public–private partnerships ensuring access to much of the area of interest. Specifically, we predicted that barred owl site occupancy rates would markedly decline across the Sierra Nevada and that site extinction/colonization would be high/low following 1 year of intensive removals. To test these predictions, we conducted collaborative experimental barred owl removals in the Sierra Nevada, monitored changes in barred owl site occupancy before and after removals using a regional-scale PAM program, and assessed spotted owl recolonization following removals as an indicator of successful recovery of native fauna.

Methods

Forging a public–private partnership

In light of the rapid growth of the Sierra Nevada barred owl population (Wood *et al*. 2020), we convened a stakeholder group representing academic researchers, state and federal agencies, and private industry. Because of the well-documented decline of the northern spotted owl caused by barred owls (Kelly *et al*. 2003; Gutiérrez *et al*. 2007; Franklin *et al*. 2021), we invoked the precautionary principle (Ashford *et al*. 1998), such that in the face of uncertainty, swift action – in the form of barred owl removals – must be taken to prevent foreclosure of future conservation options. The California spotted owl's range, and therefore the potential area threatened by invading barred owls, encompasses many landownership types, the most substantial of which are national parks, national forests, and private commercial timberlands owned by Sierra Pacific Industries (SPI). Land management mandates and objectives of the three main ownerships are preservation, multiuse conservation, and sustainable resource management, respectively. Although state-owned lands are not extensive in this region, the state of California was critical in bringing all stakeholders together to work toward the common goal of averting spotted owl population declines caused by barred owl population growth. In addition to ethical considerations and legislatively mandated conservation planning, the possibility of increased legal protections for the California spotted owl that could result from population declines incentivized this common goal. If the California spotted owl were to receive federal protection under the US Endangered Species Act (ESA), stakeholders' forest management activities, including those related to mitigating the risk of large, severe wildfires, could become considerably more time- and labor-intensive due to ESA requirements. Barred owl management on private lands was further incentivized by conservation measures associated with a Habitat Conservation Plan designed to benefit spotted owls (SPI 2020).

Surveys to locate and monitor barred owls

Barred owls and barred × spotted owl hybrids (hereafter "hybrids") were located for removals using a combination of (1) intensive passive acoustic surveys on national forests in the northern Sierra Nevada where densities are highest and (2) active broadcast surveys across public and private land across the entire Sierra Nevada. Removal success was monitored using passive acoustic surveys in the high-density northern Sierra Nevada. Although our test of the feasibility of barred owl removals focused on the northern Sierra Nevada, success in this area is likely to be indicative of the effectiveness of removals in areas of much lower density elsewhere in the Sierra Nevada.

We conducted passive acoustic surveys at 346 sites in 2018, 983 sites in 2019, and 267 sites in 2020 across 6000 km^2 of national forest land in the northern Sierra Nevada (Wood *et al*. 2019, 2020). Each site consisted of a 4-km^2 hexagonal grid cell, the approximate size of barred owl territories in the region (Figure 2; Wood *et al*. 2020). The 346 sites surveyed in 2018 were selected systematically, with approximately one of every five of the 1500 available sites receiving a survey; these sites were considered "pre-removal" in our test of removal effectiveness and provided locations of barred owls for removals. Typically, these sites were separated by at least one non-surveyed site to reduce the probability of detecting the same individuals at multiple sites (that is, to minimize false detections). The 983 sites surveyed in 2019 included 330 of those surveyed in 2018 and an additional 653 intervening sites, in order to locate as many barred owls as possible, and therefore encompassed most (65%) of the national forest lands in the northern Sierra Nevada (Figure 2). Surveys conducted in 2019 were not used to assess the effectiveness of removals (see below). The 267 sites surveyed in 2020 were a subset of those surveyed in 2018 (owing to restrictions associated with the COVID-19 pandemic) and were treated as "post-removal" sites in our test of removal effectiveness. At each site, we conducted two to five passive acoustic surveys, 5–7 nights in duration. We deployed two to three autonomous recording units (ARUs; Swift Recorder, Cornell Lab of Ornithology, Ithaca, NY) per site in areas of high topographic relief, with ARUs operating from 2000 to 0600 hours at a sample rate of 32 kHz. We scanned audio data using Program Raven Pro (v2.0; Cornell Lab of Ornithology, Ithaca, NY) and applied a previously developed sliding window template detector to our audio data to identify barred owl eight-note territorial calls (Wood *et al*. 2019). This template detector yields >0.98 probability of detecting at least one barred owl call within a bout of calling (Wood *et al*. 2019). We manually reviewed all possible detections to confirm the identification of barred owls.

Active surveys were conducted across the Sierra Nevada in areas with known, historical barred owl detections using digitally broadcasted barred and spotted owl vocalizations. We typically surveyed multiple points within 1 km of historical detections for 10 minutes each. These detections were supplemented by soliciting information on barred owl detections from management agencies and other researchers that survey for owls in the region. In concert, we expected that our passive acoustic surveys in the northern Sierra Nevada and the extensive active surveys conducted by our and other groups throughout the Sierra Nevada would locate a high fraction of the territorial barred owl population in the region.

Barred owl removals

We lethally removed barred owls and hybrids from 2018 to 2020, following field protocols established by Diller *et al*. (2014, 2016), and all removals were conducted by trained and permitted personnel from both SPI and the University of Wisconsin. Individual owls (with vertical barring on breast feathers) that produced distinct eight-note calls were identified as pure barred owls, whereas individuals (with bars and spots on breast feathers) that produced territorial calls that were neither distinctly barred owl nor spotted owl calls were identified as hybrids (see Figure S1 in Wood *et al*. [2021]).

Testing the effect of removals on barred owl occupancy

We tested for declines in barred owl occupancy following experimental removals using a multi-season occupancy model (MacKenzie *et al*. 2003) parameterized with detection/non-detection data from passive acoustic survey data from 2018 and 2020 (doi.org/10.5061/dryad.sf7m0cg5n), when removals were conducted before or after the acoustic surveys,

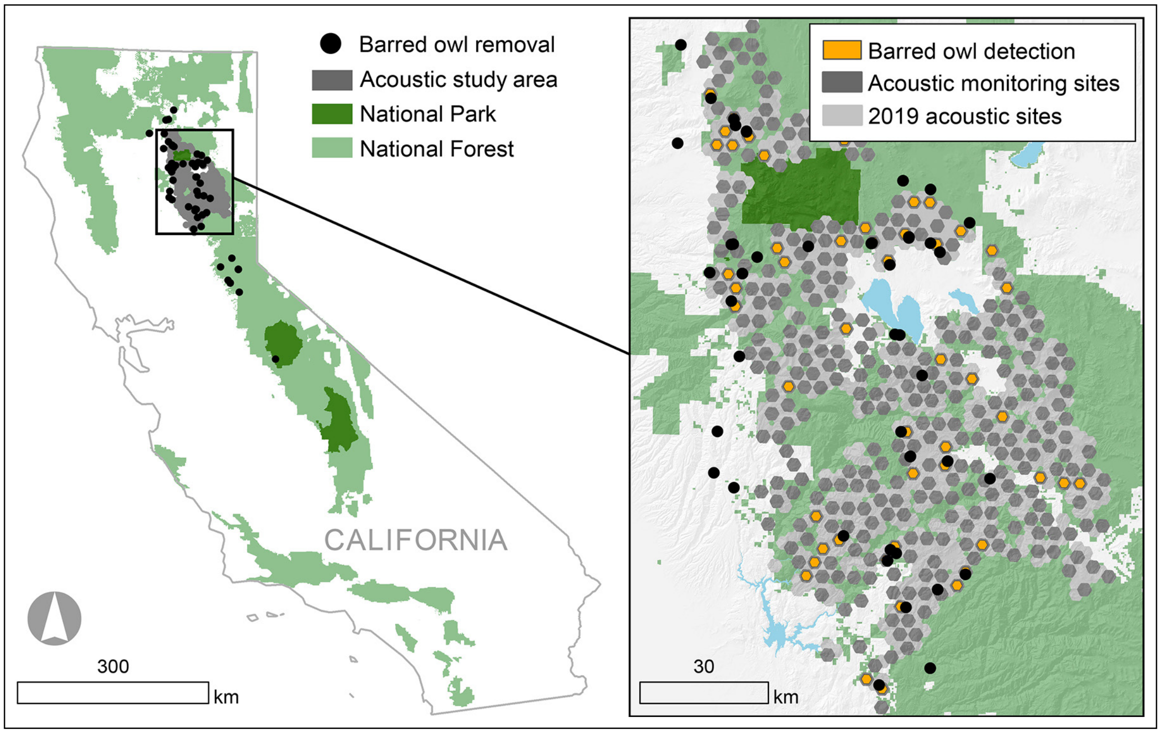

Figure 2. Removal locations of barred owl and barred owl × spotted owl hybrids from 2018 to 2020 and passive acoustic monitoring study area in the Sierra Nevada and southern Cascade Mountains, California. Inset on the right shows in dark gray the 400-ha acoustic monitoring sites that were surveyed to test the effectiveness of barred owl removals from 2018 and 2020, and in light gray the additional acoustic sites that were surveyed to locate as many barred owls as possible.

respectively. Our primary sampling periods were the two seasons (May to August, 2018 and 2020) and sites were restricted to the 267 surveyed in both the pre-removal (2018) and post-removal (2020) years. We excluded data from 2019 because removals and acoustic surveys occurred simultaneously, violating the assumption of closure. We designated two to five secondary sampling periods within each primary sampling period, which reflected the 5–7 night ARU deployments.

We estimated p (the probability of detecting a barred owl at a site given that the site was occupied), ψ (the probability of barred owl site occupancy), and ε (the probability of an occupied site going extinct from 2018 to 2020), from which we derived an estimate of γ (the probability of site colonization from 2018 to 2020). We used Akaike's information criterion corrected for small sample size (AIC_c) to compare models and considered models with $\Delta AIC_c < 2$ to have strong support from our data. We tested for heterogeneity in p between primary sampling periods (years) and among secondary sampling periods (surveys), and for changes in barred owl occupancy from 2018 to 2020 by allowing ψ to vary by year. We considered all combinations of submodel parameters to identify the model structure with the most support (Doherty *et al.* 2012). We used packages *RMark* and *xlsx* in R (v4.0.2; R Core Team 2020).

Spotted owl recolonization

We conducted active surveys using digitally broadcasted barred and spotted owl vocalizations in 2019 and 2020 at 27 former spotted owl territories (which had been occupied by spotted owls prior to 2019) after barred owls or hybrids were removed in 2019. We calculated the proportion of territories in which spotted owls were detected to assess spotted owl recolonization – and thus whether removals had prompt, direct benefits to spotted owls. Because several sites had spotted owls paired with hybrids prior to removals, we did not include those territories as being recolonized unless new spotted owls paired with the original spotted owls in the year following removals.

Results

A successful public–private partnership

Our partnership allowed access to 92% of the spotted owl's range in the Sierra Nevada. This meant that nearly all known barred owls in the region were accessible for removal, but most importantly that potential refugia for barred owls were negligible. As a result, from 2018 to 2020, we lethally removed 76 owls (63 barred owls and 13 hybrids) from the Sierra Nevada. Most removals (53) occurred within our passive acoustic survey study area (Figure 2), 12 removals occurred in a matrix of public and private land within 32 km of the surveyed area, ten occurred in the central Sierra Nevada, and one occurred in the southern Sierra Nevada.

A pronounced decline in barred owl occupancy

Barred owl site occupancy declined substantially after the initiation of removals (w = 0.56; WebTable 1; Figure 3a). Between 2018 and 2020, site occupancy decreased by a factor of 6.3, from 0.19 (85% confidence interval [CI]: 0.15–0.24) to 0.03 (CI: 0.01–0.04; Figure 3b). Site extinction was very high (ε = 0.92; CI: 0.85–0.98), site colonization was very low (γ = 0.02; CI: 0.01–0.03; Figure 3c), and detection probability was constant (p = 0.40, CI: 0.33–0.47). The second-ranked model (ΔAIC_c = 0.65, w = 0.40; WebTable 1) indicated that detection probability varied between years, but yielded an identical and substantial decline in occupancy from 2018 to 2020 as well as similar high extinction.

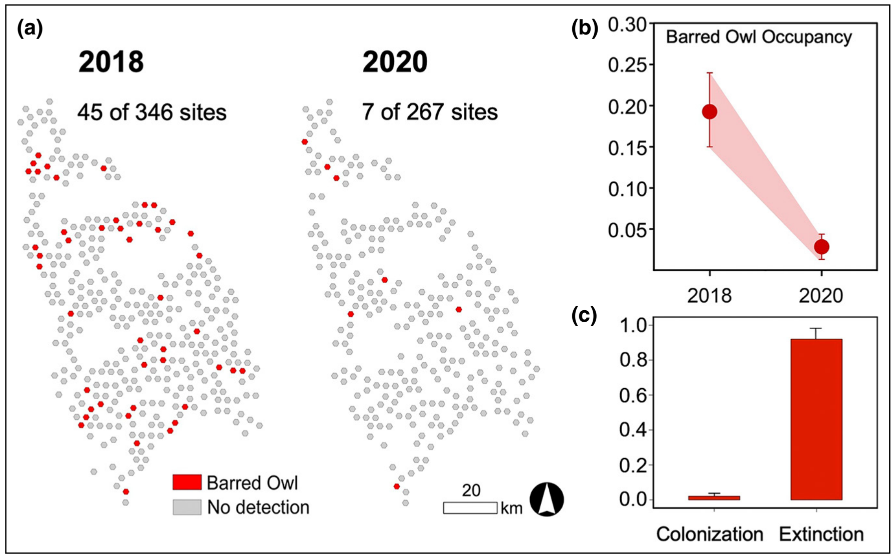

Figure 3. Acoustic detections of barred owls and barred owl × spotted owl hybrids in 2018 and 2020 (a) in the northern Sierra Nevada and southern Cascade Mountains, California. (b) Estimates of barred owl site occupancy for the pre-removal season (April to August, 2018) and post-removal season (April to August, 2020). (c) Site colonization and extinction estimates between the primary sampling periods (from 2018 to 2020), with all estimates derived from passive acoustic monitoring. The 85% confidence intervals are symbolized by the vertical bars in both (b) and (c).

Rapid spotted owl recolonization

Of 27 former spotted owl territories from which barred owls or hybrids were removed in 2019, we detected spotted owls at nine (33%) in the same season as the removals. We detected spotted owls at six additional territories 1 year after the removals, for a total of 56% recolonization (n = 15 territories) within 1 year of barred owl removals. At five of those territories, we detected paired spotted owls nesting 1 year after removals.

Discussion

Barred owl populations began to expand rapidly in the Sierra Nevada immediately prior to our removal study (Wood *et al.* 2020). However, the prominent reduction in barred owl occupancy and low recolonization by barred owls following removals demonstrates that the rapid expansion of an invasive species can be arrested even in continental systems. Moreover, extensive spotted owl recolonization of historical territories following their release from barred owl competition, sometimes within weeks of removals, and subsequent breeding demonstrates that – under certain circumstances – saving native species from extinction from an invasive competitor can be feasible. Indeed, without successful barred owl management, spotted owls will likely go extinct in California (Long and Wolfe 2019). Below we describe the four factors that contributed to successfully arresting the expansion of barred owls in the Sierra Nevada that, in principle, may enhance invasive species management more broadly.

First, the PAM effort was made possible by the confluence of low-cost acoustic survey hardware and efficient signal processing software. This enabled us to implement a regional-scale, multispecies PAM program that could be justified by its utility for monitoring populations of native species, rather than as a standalone surveillance program (Wood *et al.* 2019). As technological advances, such as PAM and eDNA, facilitate the cost-effective detection of dispersing individuals, it will likely become easier to identify invasive species before they become established. Notably, multispecies monitoring programs also enable adaptive management by allowing managers to track the efficacy of removals and the response of native fauna. Beyond technological advances, the rapid proliferation of citizen-science programs will likely facilitate economic real-time monitoring and provide an early alert system for invasive species control for a broad range of taxa (McKinley *et al.* 2017).

Second, our findings provide compelling support for implementing invasive species management as early as possible (Simberloff *et al.* 2005; Diller *et al.* 2016). In the Pacific Northwest, successful control of barred owls has been limited by a longer lag between initial invasion and experimental removal (~40 years). This delay allowed barred owls to achieve much greater densities, leading to marked declines in spotted owl populations (Long and Wolfe 2019) and consequently requiring the removal of thousands of barred owls from local areas to produce even modest spotted owl recolonization (Wiens *et al.* 2020). In contrast, thanks to early intervention in the Sierra Nevada, very few barred owl removals were necessary to reduce occupancy considerably and yield substantial and rapid recolonization by spotted owls.

Third, the biogeography of the Sierra Nevada was another key to successful barred owl management. As a forested, montane region surrounded by non-forest habitat with limited habitat connectivity to source populations, the Sierra Nevada had island-like features on a continental scale (Figure 1;

Stewart-Koster *et al.* 2015). Specifically, the low colonization rate (0.02) we observed the year following removals indicated that little immigration occurred through the narrow, forested corridor to the north and across surrounding non-forested areas despite high barred owl densities in likely source populations. Insular systems, where intervening areas can serve as natural barriers that slow invasions, are particularly suitable areas for invasive species management. Although the "defensive" strategy that we implemented requires continual intervention targeting future colonists (Simberloff *et al.* 2005), maintenance management in regions with biogeographical barriers will likely only require intermittent removals (Stewart-Koster *et al.* 2015), which has the ethical benefit of reducing the total number of individuals killed (Dubois *et al.* 2017). "Forever management" is an unfortunate reality when invasive species cannot be fully eradicated, where gains can easily be lost if resources and priorities change. However, several decades transpired before barred owls entered a phase of rapid expansion in the Sierra Nevada (Wood *et al.* 2020), suggesting that periodic removals of relatively few individuals may suffice to prevent increases from their current low densities and limit their adverse ecological effects.

Finally, public–private and trans-border partnerships can be essential to ensure the success of invasive species management in mixed-ownership landscapes, particularly in continental systems (Epanchin-Niell *et al.* 2010). In our case, we brought together a unique coalition of stakeholders to enable comprehensive land access for removals, which facilitated the removal of most known individuals across the region. However, unprecedented land access also mitigated potential barred owl refugia and thus sources for local recolonization. Therefore, we recommend that stakeholders identify common goals (eg species preservation, preventing loss of biodiversity and ecosystem services), develop incentives (eg leveraging policies intended to provide flexibility under the ESA, providing tax incentives for conservation easements), and encourage cooperation among as many relevant landowners as possible.

Conclusion

Our success illustrates several elements that can help curb the spread of invasive species on continental systems. Technological advances, such as PAM, facilitate regional-scale multispecies monitoring networks that enhance the early detection of invasive species. Incorporating biogeographic features into removal efforts can help prevent post-removal recolonization, and cross-boundary partnerships mitigate the possibility of internal invasive species refugia created by incomplete removal efforts. Employing these tactics when possible may improve the chances of successful, long-term management of invasive species in continental systems.

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Data availability statement

Data are available on Dryad (doi.org/10.5061/dryad.sf7m0cg5n).

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Supporting Information

Additional, web-only material may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/fee.2458/suppinfo