Potential trophic cascades triggered by the barred owl range expansion: Barred Owl Trophic Cascade

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Emerging Issues

Potential Trophic Cascades Triggered by the Barred Owl Range Expansion

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ABSTRACT Recently, the barred owl (*Strix varia*) has expanded its range into the Pacific Northwest of the United States resulting in pronounced effects on the demography and behavior of the northern spotted owl (*S. occidentalis caurina*). The range expansion has brought together historically allopatric species, creating the potential for significant changes in the avian predator community with possible cascading effects on food-web dynamics. The adverse effects of the barred owl on the behavior and demography of the northern spotted owl are well-documented, but little is known about the immediate and long-term effects changes in the predator community may have on native species composition and ecosystem processes. Based on northern spotted owl and barred owl selection for diet and habitat resources, there is a potential for trophic cascades within the region's predator and prey communities, differing responses by their shared and unique prey species, and possible direct and indirect effects on ecosystem processes. We explored the possible ecological consequences of the barred owl range expansion to wildlife communities of the Pacific Northwest based on the theoretical underpinnings of predator–prey relationships, interspecific competition, intraguild predation, and potential cascading trophic interactions. Negative effects on fitness of northern spotted owls because of interspecific competition with barred owls are strong selection forces that may contribute to the regional extinction of the northern spotted owl. In addition, we posit that shared prey species and those uniquely consumed by barred owls, along with other competing native predators, may experience changes in behavior, abundance, and distribution as a result of increased rates of predation by rapidly expanding populations of barred owls. © 2016 The Wildlife Society.

KEY WORDS barred owl, competition, intraguild predation, invasive species, northern spotted owl, Pacific Northwest, range expansion, *Strix occidentalis caurina*, *Strix varia*, trophic cascade.

A novel invasive predator can decrease the abundance of native predator and prey species, reduce the complexity and stability of food webs, and cause local extinctions (Finke and Snyder 2010, Ripple et al. 2014). Often, more cryptic genetic effects are coupled with these ecological effects. For example, if sufficiently abundant, invasive predators can generate significant selective pressures leading to rapid changes in abundance and distribution in phenotypic characteristics of prey and competitors. Such changes are likely if 3 criteria are met: 1) the novel predator affects the fitness of its prey and competitors; 2) some native prey genotypes are more fit than others; and 3) the selected traits of the prey species are heritable (Strauss et al. 2006).

Habitat degradation and the novel occurrence of invasive species are 2 primary factors contributing to contemporary rates of extinction and may also be powerful agents of selection for contemporary evolution (Stockwell et al. 2003). For example, in the Pacific Northwest of the United States, the recent invasion of barred owls (*Strix varia*) and loss and fragmentation of old-growth forest may combine to reduce population sizes of native species with limited adaptive responses to novel and fast-acting threats. The ability of native species to adapt to an invasive apex avian predator such as the barred owl will likely vary with species and factors such as population size, geographic distribution, gene flow, genetic diversity, and degree of local adaptation (Stockwell et al. 2003, Ghalambor et al. 2007).

Recent studies show that barred owls have expanded their populations throughout the entire geographic range of the federally threatened northern spotted owl (*S. occidentalis caurina*); in some areas, the density of barred owls is 8–10 times greater than that of historical populations of northern spotted owls (Forsman et al. 2011; Wiens et al. 2011, 2014).

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This widespread and rapid increase in abundance of a highly adaptable nocturnal predator has important conservation and management implications for northern spotted owls and other native wildlife occupying forested habitats throughout the Pacific Northwest. Herein, we identify possible direct and indirect ecological consequences following invasion of the barred owl into forest ecosystems of the Pacific Northwest. Our goal was to review and evaluate current information on potential widespread ecological changes triggered by a sharp and rapid increase in abundance of a nocturnal apex predator. Specifically, we focus on potential behavioral and adaptive changes in prey populations in response to increased predation from rapidly expanding barred owl populations. We then explore how barred owls at high density may affect ecosystem functions via indirect changes to food-web dynamics and predator–prey relationships. If native species with significant functional roles decline as a result of increased predation pressure, niche displacement, or competitive exclusion by barred owls, key ecological processes may be affected.

BARRED OWL RANGE EXPANSION

Historically, the geographic range of the barred owl was limited to forests of eastern North America, but its range has significantly expanded westward facilitated in part by human-induced land-use changes during the early 1900s (Gutiérrez et al. 2007, Livezey 2009). In the Pacific Northwest, barred owls were first detected in Washington, Oregon, and California, USA, in 1965, 1974, and 1981, respectively (Taylor and Forsman 1976, Dark et al. 1998). The range of the barred owl now completely overlaps that of the threatened northern spotted owl (Kelly et al. 2003, Gutiérrez et al. 2007, Livezey 2009), and, to a lesser extent, the California spotted owl (*S. occidentalis occidentalis*; Seamans et al. 2004). Several authors have hypothesized that barred owl dispersal and subsequent range expansion were facilitated by the creation of shelterbelts and riparian woodlands in the midwestern United States (Root and Weckstein 1994, Dark et al. 1998; see Livezey 2009 for discussion).

Regardless of its root causes, other examples of predator range expansions provide evidence of indirect human facilitation often followed by important changes in the prey community. For example, the range expansion of coyotes (*Canis latrans*) into the Olympic Peninsula of Washington State, USA, likely facilitated by the extirpation of the gray wolf (*C. lupus*), is the main driver of declines and local extirpations of the endemic Olympic marmot (*Marmota olympus*), a species of conservation concern (Witczuk et al. 2013). Similarly, the range expansion of golden eagles (*Aquila chrysaetos*) onto the Channel Islands of California, because of the introduction of wild pigs (*Sus scrofa*), resulted in a new predator of the native island fox (*Urocyon littoralis*; Roemer et al. 2002).

HYPOTHESIZED EFFECTS OF BARRED OWLS

The detrimental effects of barred owls on the demographic potential of northern spotted owls are well-documented (reviewed by Wiens et al. 2014, Diller et al. 2016). Long-term studies of northern spotted owls have shown that annual increases in the occurrence of barred owls are associated with corresponding decreases in site occupancy (Kelly et al. 2003, Olson et al. 2005, Dugger et al. 2011), apparent survival, and fecundity of northern spotted owls (Forsman et al. 2011, Wiens et al. 2014). Adverse effects of competition with barred owls were initially greatest in the northern portion of the northern spotted owl's range where barred owls were first established (Forsman et al. 2011). More recent reports indicate that barred owls have negatively affected northern spotted owls throughout their entire geographic range, with northern spotted owls experiencing an estimated range-wide decline of 3.8%/year from 1985 to 2013 (Dugger et al. 2016). The only exception was an experimental treatment area in coastal California where northern spotted owl populations began increasing following experimental removals of barred owls in 2009 (Diller et al. 2016). Exclusion of northern spotted owls from old growth forest habitats likely occurs because barred owls are behaviorally more dominant in territorial interactions (i.e., interference competition; Van Lanen et al. 2011). Their greater dispersal abilities and capacity to occur at higher densities (Wiens et al. 2011) allow barred owls to spread rapidly and exploit a common set of shared prey resources (Amarasekare 2002, Wiens et al. 2014).

Barred owls can have a strong influence on resource use and distribution of northern spotted owls, and may also be exerting strong selection pressures via direct (interference) or diffuse (exploitative) interspecific competition (Wiens et al. 2014). The ability of northern spotted owls to adapt to increased interspecific competition and direct predation may also be limited by genetic constraints arising from severe decreases in population size in some parts of the subspecies' range (Funk et al. 2010, Forsman et al. 2011). In addition, comparisons of blood parasite loads among barred owls and northern spotted owls found that northern spotted owls have greater parasite diversity and probability of infection than sympatric barred owls (Lewicki et al. 2015). These findings support the enemy release hypothesis (Torchin et al. 2003), where hosts (barred owls) benefit from a loss of parasites in their invasive range.

The barred owl range expansion into the Pacific Northwest is an ongoing process proceeding in time southward from northern Washington State to California (Gutiérrez et al. 2007, Livezey 2009). Earlier in the invasion process, Gutiérrez et al. (2007) posited that several ultimate outcomes of the range expansion of barred owls are possible, including 1) barred owls replace northern spotted owls as the dominant, nocturnal avian predator in mature and old-growth coniferous forests in the Pacific Northwest; 2) barred owls and northern spotted owls coexist in these forests but the effects of the invader on the prey community are compensatory largely because of food niche partitioning; or 3) the 2 owl species coexist but the combined effects on the prey community are additive, particularly on shared arboreal prey species. Recent studies suggest that the first outcome, competitive exclusion of northern spotted owls by barred owls throughout much of their historical range, has already begun to occur (Wiens et al. 2014, Yackulic et al. 2014, Dugger et al. 2016). Compared with spotted owls, barred owls are slightly larger (Gutiérrez et al. 2007), have more diverse diets (Hamer et al. 2001, Wiens et al. 2014), and use a broader range of forest conditions for nesting (Herter and Hicks 2000, Pearson and Livezey 2003, Livezey 2007) and foraging (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014, Singleton 2015). Barred owls also have greater survival and reproduction, and tend to use much smaller home ranges than spotted owls (Hamer et al. 2007, Singleton et al. 2010, Wiens et al. 2014). Collectively, these traits allow barred owls to reach greater densities than northern spotted owls, with the potential to exert added novel pressures on prey populations and other predators. During the transient period before competitive coexistence or exclusion evolves, for example, interspecific competition is expected to increase and the prey community may experience unprecedented rates of predation. A variety of intense behavioral interactions or adaptations by prey to increased pressure from predation may lead to novel transient dynamics within the avian predator guild and their shared food web. We created a table (Table S1, available online in Supporting Information) that shows several examples of other systems where invasive–exotic species have affected competitors, prey species, and ecosystem function.

POTENTIAL EFFECTS ON THE FOOD WEB

Changes in the abundance and distribution of apex predators can result in trophic cascades, where the effects of consumers flow down trophic levels, causing major shifts in food-web dynamics, community composition, and ecosystem processes (Estes et al. 2011, Ripple et al. 2014). Most studies examining trophic cascades have focused on how the loss of a native apex predator influences an ecosystem (Pace et al. 1999, Estes et al. 2011). In the case of the barred owl, however, the addition of a top-level consumer may also result in the restructuring of communities or potential local extinctions (Roemer et al. 2009, Ripple et al. 2013). Figure 1 illustrates the potential ecological effects the barred owl might have on the forest food webs of the Pacific Northwest.

The introduction of apex predators into an ecosystem can exert dramatic increases in top-down pressure on prey populations (Estes et al. 1998). For example, the invasive Burmese python (*Python molurus bivittatus*) in the Florida

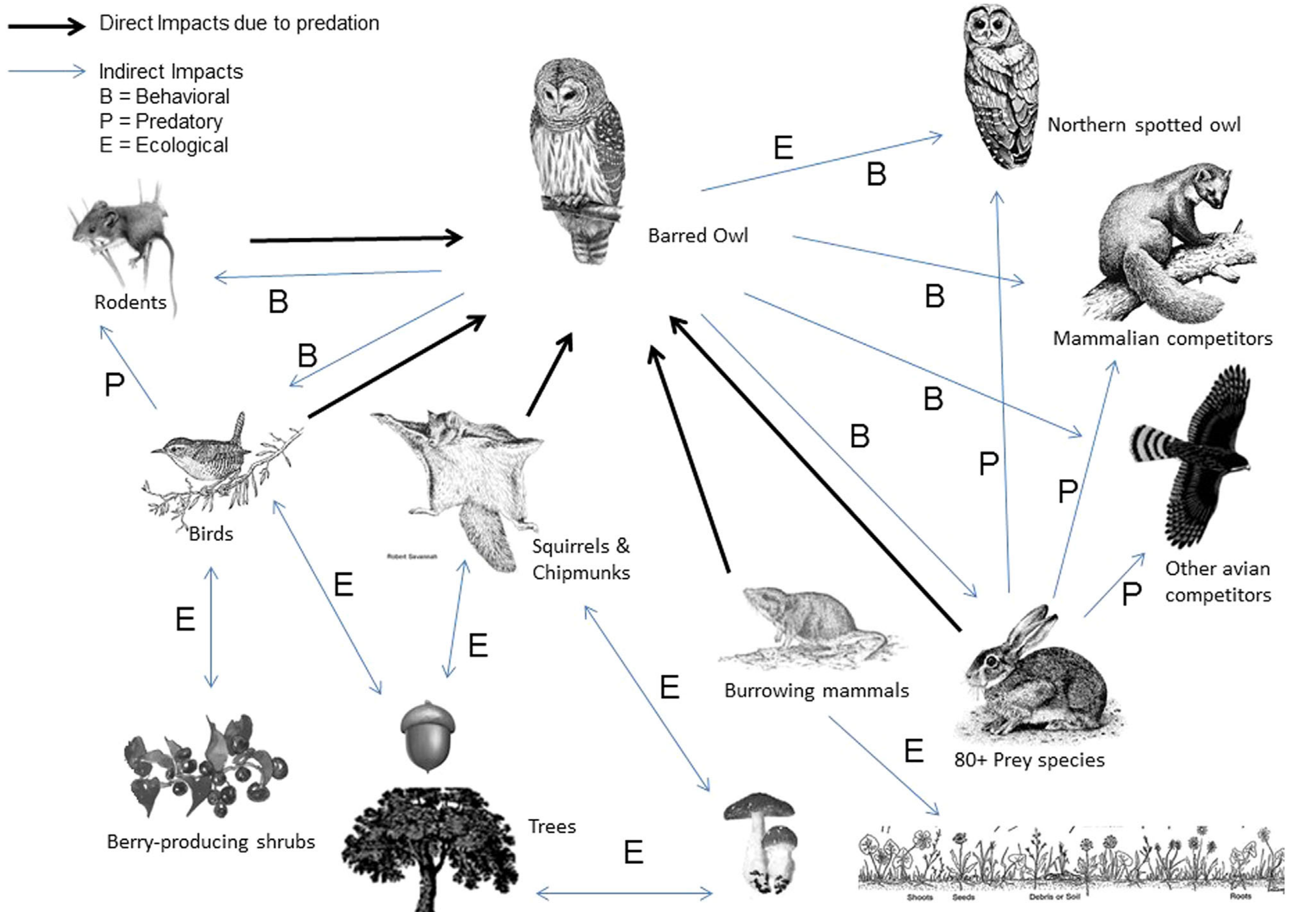

Figure 1. Direct and indirect ecological interactions that may occur within the forest ecosystems of the Pacific Northwest, United States, as a result of the range expansion of the barred owl.

Everglades (FL, USA) has caused striking declines of once-abundant mammal species (Dorcas et al. 2012). Similarly, the exotic brown tree snake (*Boiga irregularis*) on the island of Guam has rapidly decimated native bird populations, resulting in local extinctions and population declines of >90% in less than a decade (Wiles et al. 2003). If the rate of increase in barred owl populations continues, the prey community could be strongly affected, perhaps moving it toward an ecological threshold resulting in the local extinction of multiple species and loss of important ecological processes (Hewitt and Thrush 2010).

Extinctions of ecologically important species, and apex predators in particular, can have far-reaching consequences on the function and structure of an ecosystem (Borrvall and Ebenman 2006, Prugh et al. 2009). Loss of top predators may propagate through the food web setting off a cascade of secondary extinctions as the system approaches a new state (Scheffer et al. 2001, Ebenman and Jonsson 2005). Loss of species diversity and functional groups can also affect ecosystem processes (Tilman et al. 2014). The time lag between initial species loss and onset of secondary extinctions depends on the diversity of the food web, rates of dispersal among local populations that enables recolonization, and ability of species to adapt to a restructured food web (Borrvall and Ebenman 2006, Sahasrabudhe and Motter 2011).

Trophic linkages that could potentially be disrupted by barred owls are highlighted by recent dietary studies conducted within the invasive portion of the barred owl's geographic range. In the Oregon Coast Range and northwestern Washington State, for example, the primary prey items of barred owls in terms of contributions to dietary biomass included northern flying squirrels (*Glaucomys sabrinus*), tree voles (e.g., *Arborimus longicaudus*, *Myodes californicus*, *Microtus oregoni*), lagomorphs (*Lepus americanus*, *Sylvilagus bachmani*), moles (*Scapanus* spp.), tree squirrels (*Tamiasciurus douglasii*, *Sciurus griseus*), shrews (*Sorex* spp.), and woodrats (*Neotoma fuscipes*, *N. cinerea;* Hamer et al. 2001, Graham 2012, Wiens et al. 2014). Mammals comprised 65–76% of prey numbers and 75–89% of prey biomass in diets of barred owls in the Oregon Coast Range and northwestern Washington State (Hamer et al. 2001, Wiens et al. 2014), which is comparable to the percent of mammal prey numbers estimated by studies conducted in other portions of the barred owl's range (71%; reviewed by Livezey 2007). The remainder of the diet of barred owls in Oregon and Washington consisted of >30 species of birds, frogs (*Lithobates* spp.), salamanders (e.g., *Ambystoma* or *Dicamptodon* spp.), lizards (e.g., *Elgaria coerulea*, *Sceloporus occidentalis*), snakes (*Thamnophis* spp.), crayfish (*Pacifastacus leniusculus*), multiple species of snails, fish (*Osteichthyes* spp.), and large numbers of ground beetles (mainly *Pterostichus lama*, *Carabidae* and *Pterostichus* spp.; Hamer et al. 2001, Graham 2012, Wiens et al. 2014). Barred owl diets in the Pacific Northwest are similar to diets in the eastern portion of their range, with the exception that eastern populations of barred owls appear to capture greater numbers of species associated with riparian and aquatic environments, including crayfish, fish, and amphibians; Livezey 2007, Wiens et al. 2014). Diets of barred owls appear to vary among geographic regions according to disparities in the distribution of preferred prey, latitudinal changes in prey species diversity, or temporal variation in prey use and availability among regions (Graham 2012, Wiens et al. 2014).

Barred owls now greatly outnumber northern spotted owls in Washington and Oregon (3–8 barred owl territories/northern spotted owl; Hamer et al. 2007; Singleton et al. 2010; Wiens et al. 2011, 2014), and, to a lesser extent, northern California spotted owls (Diller et al. 2016, Dugger et al. 2016). Given that barred owls now occur in greater densities than historical populations of northern spotted owl, it is clear that barred owls are not a direct functional replacement of northern spotted owls in forested ecosystems of the Pacific Northwest. Moreover, as a generalist predator, barred owls capture a greater proportion of diurnal, terrestrial, and aquatic prey than northern spotted owls, which specialize on arboreal and semiarboreal prey such as northern flying squirrels, red tree voles (*A. longicaudus*), and woodrats (Forsman et al. 2004, Wiens et al. 2014). In addition, because barred owls use a greater diversity of forest types and other habitats including meadows, swamps, and riparian areas, a wider range of prey species may be affected if they replace northern spotted owls (Hamer et al. 2001, 2007; Wiens et al. 2014). Theoretically, reductions of northern spotted owl populations may release pressure on sensitive arboreal prey species associated with older forest types, but this potential release will likely be offset by the greater density of barred owls that prey on the same species (Wiens et al. 2014). Therefore, we hypothesize that expanding barred owl populations will result in increased predation pressure on traditional and naïve prey species within the range of the northern spotted owl.

Initially, the largest declines in the prey community might be expected for primary prey species used by both northern spotted owls and barred owls, such as northern flying squirrels, red tree voles, and lagomorphs. As the densities of selected prey species are reduced, however, both owl species might switch to more available alternate prey species (Fernandez 1993). For example, in part of its eastern native range, barred owls consumed more cottontail rabbits (*Sylvilagus floridanus*) when their preferred rodent prey species, hispid cotton rats (*Sigmodon hispidus texianus*), were less available as a result of cyclic population trends (Korschgen and Stuart 1972). Prey-switching behavior has the potential to stabilize or destabilize the food web (Post et al. 2000), but would likely favor the barred owl as a generalist predator.

Prey species that evolved with an avian predator are not naïve to predation, but may decline in number because of the widespread distribution of a newly established predator that occurs at a greater density than other native predators. Within their newly extended range, barred owls capture a variety of aquatic prey species not previously exposed to a nocturnal avian predator at high densities (U.S. Fish and Wildlife Service 2013, Wiens et al. 2014, Diller et al. 2016). Susceptible prey species naïve to this new predation pressure, particularly amphibians and small mammals, may experience increased rates of mortality unless they can quickly develop avoidance behaviors in the presence of a newly established and widespread predator.

The adaptive potential of prey species to respond to increased predation rates will be related to their local population sizes, geographic distribution, and genetic variability. If prey populations are large and genetically diverse, additive increases in predation by barred owls may lead to changes in the distribution of prey phenotypes. Prey species may also attempt to evade the barred owl by moving out of selected habitats or by adopting other avoidance behaviors (Chivers et al. 2001, Losos et al. 2004). Elsewhere, for example, nonlethal effects of perceived predatory risk from barred owls led to changes in space use by white-footed mice (*Peromyscus leucopus*), which had an indirect, cascading effect on predation rates of veery (*Catharus fuscescens*) songbird nests (Schmidt 2006; Fig. 1). Predation by an invasive nocturnal predator may also lead to changes in communication behavior in native species. For example, veery adjusted their diurnal singing behavior when exposed to broadcast vocalizations of barred owls (Schmidt and Belinsky 2013; Fig. 1). Because of phenotypic plasticity, in a relatively short timeframe, it is possible that the barred owl's aquatic prey species may develop predator-induced defenses triggered by water-borne alarm pheromones released by attacked conspecifics (McCollum and Leimberger 1997). It would likely take a much longer amount of evolutionary time for land-based prey species to eventually develop inducible morphological defenses against the barred owl, such as cryptic coloration or methods to evade attacks (O'Steen et al. 2002, Moore et al. 2004). Increased predation rates may cause prey species to alter their life-history strategies to increase overall fitness—for example, by allocating more energy toward total reproductive output (Reznick and Endler 1981, Moore et al. 2004, Barribeau et al. 2010).

POTENTIAL DECLINE IN SENSITIVE SPECIES

Three mammal and one bird species, known prey of the barred owl in western Oregon, are listed as sensitive species in the Pacific Northwest (U.S. Fish and Wildlife Service 2013, Wiens et al. 2014). These are the western gray squirrel (*S. griseus*), western pocket gopher (*Thomomys mazama*), red tree vole, and band-tailed pigeon (*Patagioenas fasciata*). Based on frequency of occurrence in diets of barred owls in the Pacific Northwest (Hamer et al. 2001, Graham 2012, Wiens et al. 2014), mammal species with limited distributions (e.g., red tree voles, northern flying squirrels, woodrats, pocket gophers) may be especially susceptible to increases in predation rates. Further, other sensitive species, potential prey or competitor species, occur within the expanded range of the barred owl in the Pacific Northwest (U.S. Fish and Wildlife Service 2013). Most sensitive species have small population sizes and may lack genetic variation as a result of random genetic drift and inbreeding (Stockwell et al. 2003). Limited genetic diversity may translate into a lack of adaptive potential to survive a novel stressor such as increased rates of predation.

Prey species that are both locally abundant and widely distributed may support large predator densities, leading to greater depredation on sensitive species through asymmetrical apparent competition (Holt 1977). In apparent competition, when 2 prey species share a common predator, an increase in 1 prey species will cause the predator's population size to rise, indirectly resulting in a decrease in the other prey species (see DeCesare et al. 2010). Native predators that are already experiencing population declines due to habitat loss, such as the northern spotted owl, may also be adversely affected by increases in apparent competition. For example, great horned owls (*Bubo virginianus*) prey upon both northern spotted owls and barred owls. Increasing densities of barred owls in the Pacific Northwest may lead to increased predation pressure on northern spotted owls and other species associated with older forests by displacing them into more open habitats favored by predators such as great horned owls and red-tailed hawks (*Buteo jamaicensis;* Wiens et al. 2014).

PONTENTIAL EFFECTS ON THE PREDATOR COMMUNITY

Predator guilds are essential in ecological communities because they can facilitate energy and nutrient transfer, stabilize or destabilize food webs, and produce cascading trophic effects (Ritchie et al. 2012, Lesmeister et al. 2015). If a novel predator successfully invades an ecosystem occupied by a native predator with overlapping niche requirements, interspecific competition may result in competitive exclusion. Alternatively, coexistence may be achieved through ecological character displacement expressed as morphological, ecological, behavioral, or physiological differences between species (Strauss et al. 2006). Such differences may reduce the strength of competition and allow for a dynamic coexistence when resources are not strongly limiting. However, given the rapid rate of increase in density of the barred owl in its expanded range, coupled with the life history and genetic constraints linked to a small population size, and depressed demographic potential of the northern spotted owl, it is unlikely that niche complementarity will evolve between these species (Gutiérrez et al. 2007, Wiens et al. 2014).

Displacement of the northern spotted owl by the barred owl is also predicted by intraguild predation theory. Intraguild predation, the most extreme form of interference competition, is the killing and eating of a species that uses and competes for similar resources (Polis et al. 1989, Polis and Holt 1992) and is widespread in raptor assemblages (Sergio and Hiraldo 2008). The nocturnal avian predator guild in the Pacific Northwest includes the great horned owl, barred owl, northern spotted owl, northern saw-whet owl (*Aegolius acadicus*), and western screech owl (*Megascops kennicotti*). Our focus here is on effects of predation of northern spotted owls by barred owls, but we note that evidence exists for local extinctions of western screech owl populations as a potential consequence of intraguild predation by barred owl (Elliot 2006, Acker 2012). Although barred owls are rarely observed killing and eating northern spotted owls, they often attack northern spotted owls as shown by multiple observations (Gutiérrez et al. 2007, Wiens et al. 2014) and call-playback experiments (Van Lanen et al. 2011). For both species to coexist, the intraguild prey (northern spotted owl) must be superior at exploiting shared resources and competitively dominant (Polis and Holt 1992, Holt and Polis 1997). Neither of these conditions are met in the barred owl–northern spotted owl case.

Rapid increases in the distribution and abundance of barred owls could indirectly lead to declines of other predators in the Pacific Northwest that share common prey species (Fig. 1). Continuing increases in barred owl populations could lower the carrying capacity for sympatric competitors or force shifts in diet or habitat use. Native avian predators, such as the Cooper's hawk (*Accipiter copperii*), northern goshawk (*A. gentilis*), western screech owl, sharp-shinned hawk (*A. striatus*), red-shouldered hawk (*Buteo lineatus elegans*), and great horned owls, all have potential diet overlap with the barred owl. In the eastern part of its range, the barred owl has extensive diet overlap with other owl and raptor species (Bosakowski and Smith 1992). The greatest diet overlap occurs between the eastern screech-owl (*M. asio*), and 3 *Buteo* hawks (red-shouldered hawk, red-tailed hawk, and broad-winged hawk [*B. platypterus*]), which are all species that select small mammal prey, have similar body sizes, and share a perch-hunting strategy (Bosakowski and Smith 1992). Sympatric raptors with extensive diet overlap often achieve coexistence if their body sizes, predation modes, activity rhythms, or use of habitats are sufficiently different (Gutiérrez et al. 2007)—for example, coexistence between the upland buzzard (*Buteo hemilasius*) and the Eurasian eagle owl (*Bubo bubo*) in the Tibetan Plateau (Qinghu et al. 2008). Populations of native raptor species whose diets overlap with invading barred owls in the Pacific Northwest may experience declines as the carrying capacity of the environment declines, but local extirpations of these species are unlikely given that they historically co-exist with barred owl in eastern North America.

Significant diet overlap can also occur among sympatric predators from different taxonomic classes, especially between generalist species that forage opportunistically (Pascoe et al. 2011). In the Pacific Northwest, native mammalian carnivores, such as the fisher (*Martes pennanti*) and American marten (*M. americana*), may experience exploitative competition with barred owls because these species are also largely nocturnal, share habitats, and exploit strikingly similar prey species including voles, deer mice (*Peromyscus maniculatus*), shrews, and lagomorphs (Buskirk and MacDonald 1984, Zielinski and Duncan 2004; Fig. 1). The potential competitive relations between barred owls and *Martes* species are especially relevant to efforts to reintroduce *Martes* to areas in the Pacific Northwest where extirpation has occurred (Aubry and Lewis 2003).

Barred owls may have significant direct and indirect effects on native mesopredators through predation or interference competition. Smaller avian mesopredators, such as the northern saw-whet owl, northern pygmy owl (*Glaucidium gnoma californicum*), and western screech owl, have been documented in the diets of both northern spotted owls (Forsman et al. 2004) and barred owls (Hamer et al. 2001, Elliot 2006, Wiens et al. 2014). Western screech owls, in particular, may be experiencing sharp declines in numbers in response to rapid increases in barred owl populations in the Pacific Northwest (Elliot 2006, Acker 2012). Mesopredators may avoid certain areas because of the presence of barred owl nest sites and the threat of predation—for example, black kites (*Milvus migrans*) avoid eagle owl territories in Italy (Sergio et al. 2003). The consumption of mesopredators by apex predators is common in raptors and influenced in part by the abundance, distribution, and availability of primary prey (i.e., food-stress hypothesis; Lourenco et al. 2011, also see review by Sergio and Hiraldo 2008). As barred owl populations continue to increase, the decreasing availability of shared prey species may lead to dietary shifts that indirectly influence other avian mesopredators. For example, nonlethal effects due to predation risk might decrease overall availability of shared food resources if the behavior of small mammal prey is altered by the presence of barred owl (Schmidt 2006, Schmidt and Belinsky 2013).

The ability of potential competitors to adapt to the recent invasion of the barred owl may be related to their degree of phenotypic plasticity (Ghalambor et al. 2007). Adaptive variation in response to different environmental conditions may allow genotypes to establish populations in new environments without additional costs to fitness. As barred owl abundance and distribution increase in the Pacific Northwest, generalist competitors that utilize a variety of habitats and prey might be expected to respond less negatively to the invasion than sympatric specialist predators such as the northern spotted owl.

POTENTIAL INDIRECT EFFECTS ON ECOSYSTEM PROCESSES

Stability in ecosystem processes requires sustaining a full complement of ecological functions by maintaining the composition and relative abundances of native species (Tilman et al. 2014). However, differences in diet, home range size, demography, and behavior demonstrate that the barred owl are not a direct functional replacement for the northern spotted owl in forested ecosystems of the Pacific Northwest. As a consequence, we anticipate changes in ecosystem properties and processes. Increases in the distribution and abundance of barred owl populations may have cascading effects across multiple tropic levels and potentially trigger ecosystem changes at large spatial scales.

Potential Decline in Tree and Shrub Growth and Establishment

As a result of their tendency to hoard and cache seeds, many squirrel and bird species are effective seed dispersers with significant effects on the establishment of numerous woody plant species (Wenny 2001, Steele et al. 2005; Fig. 1). Douglas' squirrel (*T. douglasii*), northern flying squirrel, western gray squirrel, and Steller's jay (*Cyanocitta stelleri*)—known prey species of the barred owl (Hamer et al. 2001, Wiens et al. 2014)—are important dispersal agents for multiple tree species in the Pacific Northwest. Birds often fill major ecological roles as seed dispersers for fruiting plants by improving seed germination

(Meyer and Witmer 1998) and the likelihood of establishment (Garcia et al. 1999; Fig. 1). For example, migratory European thrush (*Turdus* spp.) populations contribute significantly to the conservation and restoration of the Spanish juniper (*Juniperus thurifera*) because of their role as seed dispersers (Telleria et al. 2011). In western Oregon, there are ≥7 frugivorous bird species that have been identified in the diet of barred owls (Wiens 2012). If these species experience population declines as a consequence of barred owl predation, decreased establishment and growth of shrub and tree species may occur.

Tree squirrels in the Pacific Northwest consume truffles as a major part of their diet (Maser et al. 1978). Truffles are the spore-producing bodies of mycorrhizal fungi, which have a symbiotic relationship with the roots of many forest trees (Carey 2004). This symbiosis is critical for efficient nutrient acquisition, protection against root pathogens (Smith et al. 2005), and efficient water intake (Conner 1988). Hypogeous mycorrhizal fungi are dependent on small mammals as the primary means of spore dispersal (Maser et al. 1978; Fig. 1). The northern flying squirrel has been considered a keystone species in forests of the Pacific Northwest in part for this reason, but also because of the importance of the squirrel as prey for northern spotted owls and many other native predators (Carey 1995, Carey et al. 2002). A meta-analysis of northern flying squirrel densities throughout North America demonstrate that forest management has a large effect on squirrel populations, and like northern spotted owls, northern flying squirrels inhabit mature, uncut forests (Holloway and Winston 2011). Given that northern flying squirrels are a primary contributor to dietary biomass of barred owl in the Pacific Northwest (Hamer et al. 2001, Graham 2012, Wiens et al. 2014), we posit that sharp increases in predation are likely as barred owls increase in abundance. In this scenario, increases in populations of barred owls leading to decline in tree squirrel abundance could indirectly lead to reduced recruitment and growth of both old-growth and managed forests that rely on squirrels for spore dispersal.

Potential Decrease in Soil Processing

As a result of potential increased depredation by barred owls, one anticipated change in the Pacific Northwest is a decline in populations of burrowing small mammals leading to declines in the rates of decomposition of organic matter and litter, and mixing of forest soil (Pearce and Venier 2005). Burrowing small mammals are considered ecosystem engineers that modify, maintain, and create habitats by significantly altering the physical environment (Huntly and Inouye 1988, Reichman and Seabloom 2002). Their extensive tunnel systems also provide important refugia for a variety of other small mammals, amphibians, reptiles, and insects (Maser 1998). Overall, in the Oregon Coast Range, the barred owl preys on ≥17 small mammal species that provide important services to Pacific Northwest ecosystems (Wiens et al. 2014).

PRIORITIES FOR RESEARCH AND MANAGEMENT

Invasive predators often reach greater population densities than native predator species and have greater effects on shared prey species (Finke and Snyder 2010). In addition, during the period of invasion, total predator densities may be greater with unprecedented rates of predation. Even small changes in the relative strength of competition among species may significantly alter interspecific interactions and ecosystem function (Carey et al. 2012); therefore, the advancing barred owl invasion is predicted to result in significant changes in the prey community, food webs, and ecosystem processes.

The conditions for coexistence between northern spotted owls and barred owls—niche complementarity and resource partitioning—appear unlikely (Gutiérrez et al. 2007, Dugger et al. 2011, Wiens et al. 2014, Yackulic et al. 2014). The diet of the northern spotted owl is largely included within that of the barred owl (Hamer et al. 2001, Wiens et al. 2014). In addition, a critical condition for coexistence—that is, the species whose niche is included must be a superior competitor to the more generalized species (Chase 1996)—is likely not satisfied in this case. On the basis of multiple factors, including predictions from intraguild predation theory, smaller area requirements, and the barred owl's greater demographic potential, body size, population density, and diet breadth, the most likely outcome in the Pacific Northwest is eventual local extinction of the northern spotted owl and replacement by the barred owl.

In an effort to determine whether control of barred owl numbers is an effective conservation tool to benefit northern spotted owls, the U.S. Fish and Wildlife Service recommended experimental removal of barred owls to facilitate recovery of northern spotted owls (U.S. Fish and Wildlife Service 2011). Barred owl removal experiments can provide a direct test of the significance of interspecific competition with northern spotted owls (Buchanan et al. 2007, Gutiérrez et al. 2007), increase our understanding of the ecological interactions between the species (Wiens et al. 2014), and allow for the evaluation of the cost-effectiveness and feasibility of barred owl removal at local scales (Diller et al. 2014). In addition, many of the hypotheses we put forward concerning potential trophic dynamics could be directly tested if the removal of barred owls followed a rigorous experimental design including replication and control and treatment areas (U.S. Fish and Wildlife Service 2013).

Recommendations to conduct experimental removal of barred owls have been criticized as being too difficult to accomplish because of the effort and cost required to maintain sufficiently low numbers of barred owls to benefit northern spotted owls (Livezey 2010, Rosenberg et al. 2012). Nonetheless, pilot studies in coastal California have demonstrated a positive association between removal of barred owls and population trends of northern spotted owls (Diller et al. 2016, Dugger et al. 2016); Diller et al. (2014) reported that removal of barred owls can be rapid, technically feasible, and cost-effective. Following barred owl removal efforts, displaced northern spotted owls have been able to recolonize their original or adjacent territories (Diller et al. 2014, 2016). If barred owl removal is conducted alongside of habitat conservation and management, then it may be possible to slow or reverse local northern spotted owl population declines (Diller et al. 2014, 2016; Dugger et al. 2016).

Population control of native North American species that have become invasive in areas where they have been introduced or have expanded their range is already established for other species such as the American bullfrog (*Lithobates catesbeiana*) in the western United States and sea lamprey (*Petromyzon marinus*) in the Great Lakes (USA). These control efforts may be indeterminate in some cases, but they reduce invasive populations to ensure the persistence of sensitive species (such as the northern leopard frog [*Lithobates pipiens*] in the case of the American bullfrog). We note, however, that removal efforts that focus on reducing an invader's presence ('control'), or their spread ('containment'), can be indefinite and expensive (Zavaleta et al. 2001).

In the Pacific Northwest, complete eradication of barred owls is unlikely because of their abundance and colonization and dispersal abilities (Rosenberg et al. 2012; Yackulic et al. 2012, 2014). However, removal over large scales may affect regional occupancy rates and lead to reduced barred owl recolonization (Yackulic et al. 2012). Projections from occupancy models suggest that maintaining barred owls at a relatively low occupancy level (~0.2/survey polygon) may decrease competition and benefit northern spotted owls by significantly lowering barred owl colonization rates (Yackulic et al. 2014). Removal efforts may be most effective if they are focused in areas that already have a low barred owl population, defensible to barred owl colonization, have high-quality habitat for northern spotted owls or other sensitive barred owl prey species, or slated for reintroduction efforts for barred owl competitors such as the fisher and American marten.

Barred owl removal experiments provide a unique opportunity to test multiple hypotheses broadly relevant to community ecology, food-web theory, and the role of top-down predation effects on trophic dynamics. For future research, we recommend studying the potential population declines in barred owl prey species and comparing population densities of prey species that occur in both east and west portions of the barred owls' range. Other areas of potential study include the possible diet and habitat shifts of barred owl competitors, along with changes in tree growth and establishment and soil processing. Although research has focused on the northern spotted owl so far, particular interest should be placed on the other sensitive species that will be affected by the barred owl invasion in the Pacific Northwest.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Table S1. Examples of the effects of nonnative predators on native prey species, and ecosystems.