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Influence of forest disturbance on bobcat resource selection in the central Appalachians

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ABSTRACT

Similar to trends across the eastern United States, the central Appalachian Mountains were nearly entirely deforested by the early 20th century, then regenerated with a drastically altered disturbance regime. Forests found across much of the region today share little resemblance to the forest communities in which native wildlife evolved, including bobcats (*Lynx rufus*), a species adapted to stalking and ambushing prey in dense concealment cover. Managers implement efforts to restore historical forest structure and create wildlife habitat using prescribed fire, timber harvest, and maintained clearings. We developed resource selection functions utilizing GPS telemetry data from 9 bobcats (6 male, 3 female) monitored in 2018–2019 to investigate how prescribed fire, timber harvest, and forest edge may influence 3rd order (i.e. within home range) resource selection of bobcats in the Appalachian Mountains of western Virginia, USA. We found that bobcats selected for forest-edge, fire-created canopy openings, and recently harvested forest stands, and avoided the forest interior. Bobcats are likely selecting for these areas because of increased prey and cover. The comparatively widespread use of fire in this study area has allowed novel insight into the effects of prescribed fire on bobcat space use and demonstrates the ecological importance of future efforts to restore historical fire cycles in the Appalachians. As one of the largest carnivores in Appalachian ecosystems and the only wild felid remaining in the region, we suggest managers consider bobcat ecology when planning habitat management strategies and communicate those strategies to the public. Our results demonstrate that silvicultural practices that aim to mimic historical forest disturbance likely benefit native wildlife, as evident from selection of these treatments by bobcats in this system.

1. Introduction

In forest restoration, rehabilitation refers to the restoration of desired species composition, structure, or processes, in a degraded, but existing ecosystem (Stanturf et al., 2014). Forest rehabilitation efforts are typically conducted at the primary producer level of ecosystems (i.e. forestry practices), yet evaluations of their efficacy should span multiple trophic levels (Keddy and Drummond, 1996). Top predators can be an indicator of the influence of forest restoration efforts on ecological processes, because a response from a top predator likely indicates responses at multiple trophic levels.

The forested ecosystems of the central Appalachian Mountains (hereafter Appalachians) have undergone dramatic shifts in structure and composition over recent centuries, primarily beginning with European settlement and increasing over time (Davis, 2003). Many pre-settlement Appalachian forests consisted of a patchwork of uneven-aged stands, which were shaped by complex disturbance regimes (Abrams et al., 1995, Abrams and McCay, 1996, Flatley and Copenheaver, 2015). Historically, one of the most important disturbance mechanisms was fire, which was frequent and widespread throughout much of the Appalachians (Lafon et al., 2017). Most pre-settlement fires consisted of low to mixed-severity burns that created open, park-like forests, with a lower density of trees than modern forests (Nowacki and Abrams, 2008). Elk (*Cervus canadensis*) and bison (*Bison bison*) were also present on the landscape, both of which can profoundly influence plant communities (Knapp et al., 1999, Roberts et al., 2014).

By the early 20th century, unregulated timber harvest followed by uncontrolled, intense burning culminated in near-total deforestation throughout the region, and elk and bison were extirpated from the landscape (Brooks, 1965, Davis, 2003). Over the past century, forests have

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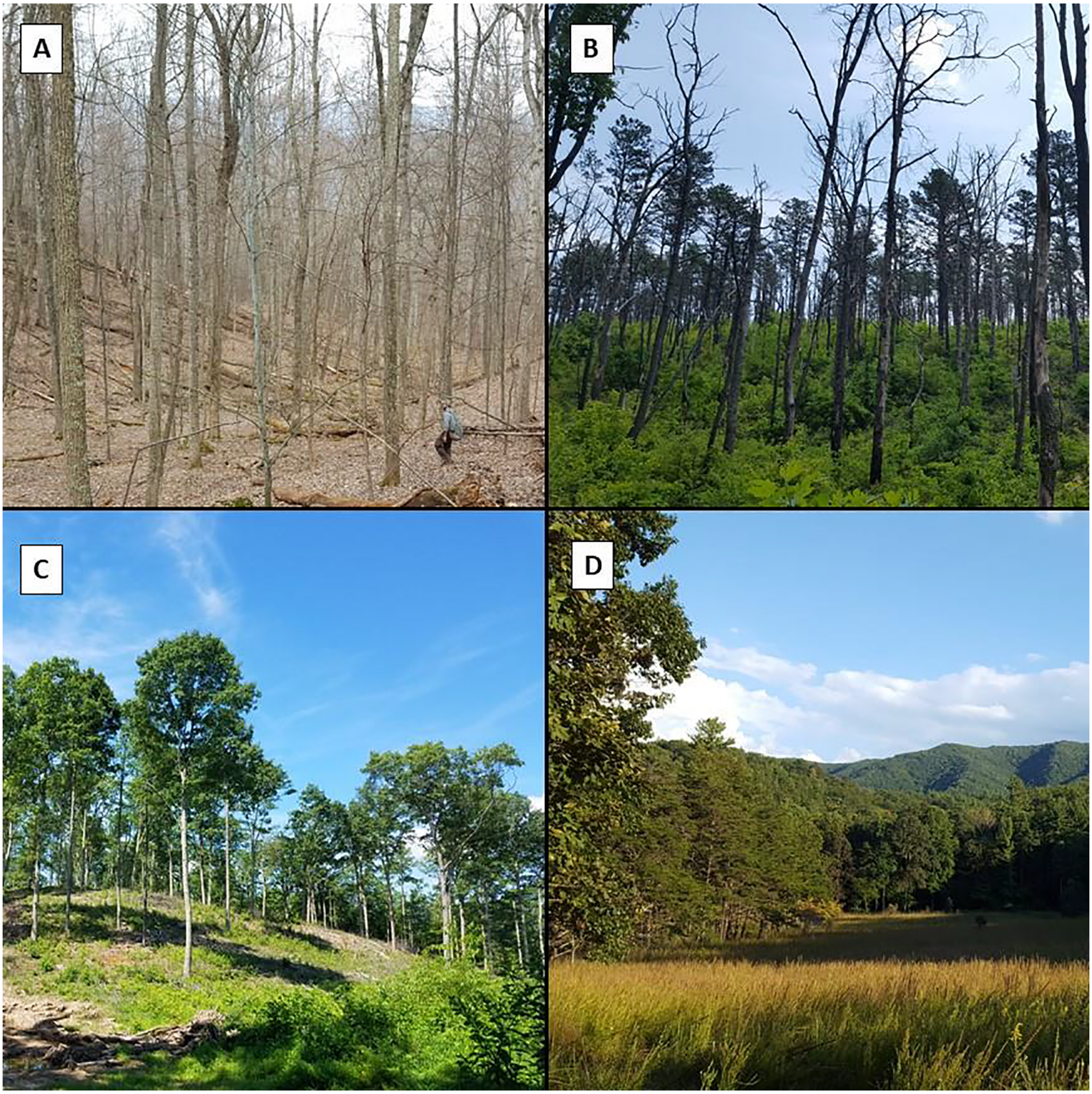

Fig. 1. Panel A shows the interior of a densely-stocked and even-aged forest, with researcher for scale. Panel B shows an area of fire-created canopy openings on National Forest, as part of a much larger mixed-severity fire. Panel C shows a recent shelterwood timber harvest on a state Wildlife Management Area. Panel D shows a wildlife clearing on National Forest. Images by DCM.

regenerated throughout much of the Appalachians, yet largely in the absence of native grazers or broad-scale disturbance. Notably, these forests have regenerated during an era of fire suppression, despite the crucial role of frequent fire in shaping and maintaining historic Appalachian ecosystems (Lafon et al., 2017). The absence of fire appears to be spurring a broad shift from oak (*Quercus* spp.) forests to those dominated by maple (*Acer* spp.) and other mesophytic plant species, a process termed mesophication (Nowacki and Abrams, 2008). More recently, changes in timber harvest strategies, agricultural practices, and the distribution of human populations have contributed to decreases in young forests throughout the eastern United States (Trani et al., 2001). Additionally, the concurrent introduction and proliferation of numerous exotic pests and pathogens continue to drastically alter forest ecosystems in eastern North America (Lovett et al., 2006). These patterns of regeneration have led to the wide-scale maturation and mesophication of eastern forests, resulting in contiguous swaths of mature, even-aged forest with relatively bare understory, and decreases in mast-producing overstory species (Nowacki and Abrams, 2008, Trani et al., 2001; Fig. 1A).

In the face of these broad-scale patterns, land managers in the Appalachians have been implementing measures to restore historical forest structure and create wildlife habitat through timber harvest, mowing, herbicidal treatments, and increasingly, through the use of prescribed fire. Particularly on United States Forest Service (USFS) lands, managers in the region are increasing their use of prescribed fire, with the primary goals of restoring Appalachian mixed-oak ecosystems, enhancing wildlife habitat, and reducing fuel loads (Brose et al., 2001, Brose et al., 2013, Lorber et al., 2018; Fig. 1B). Converse to the increasing use of prescribed fire, the scale of timber harvest conducted by the USFS has declined in recent decades, resulting from shifts in societal values and administrative policies within the USFS during the early 1990 s (Oswalt et al., 2009). Public perception of timber harvest and prescribed fire can be negative, which has potential to drive management

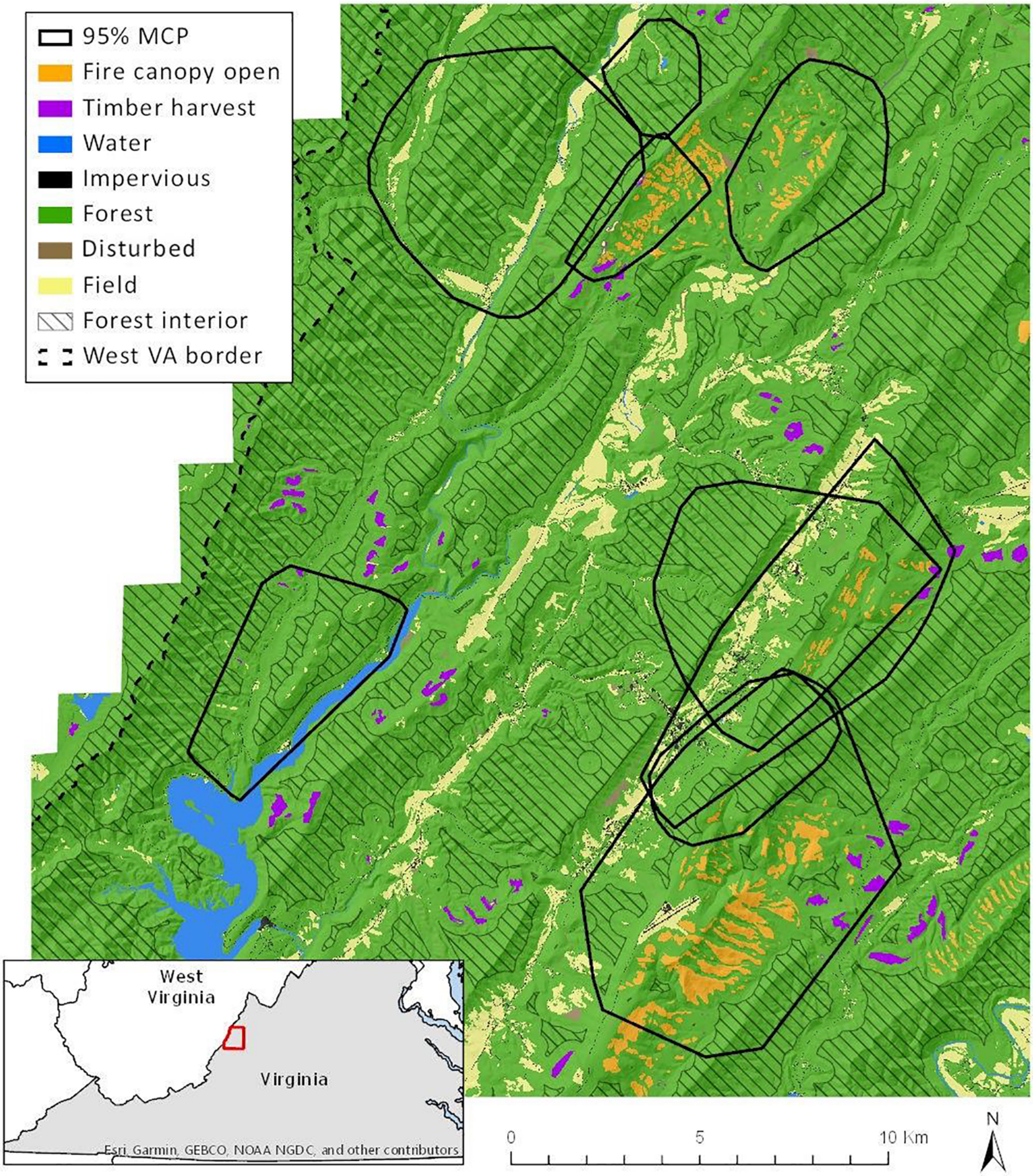

Fig. 2. Map of study area in Bath County, Virginia showing areas of fire-created canopy openings, timber harvest, other disturbed areas, fields, forest interior, and other land cover categories. Included are 95% minimum convex polygons (MCP) of the 9 bobcats used in this analysis that were collared from 2018 to 2019.

and policy involving these practices (Bliss, 2000, Manfredo et al., 1990). As the quantity of timber harvest has decreased, the goal of timber harvest on USFS lands has shifted from being more strictly focused on timber production to an emphasis on the creation of wildlife habitat, among other ecologically focused goals (Oswalt et al., 2009, Fig. 1C). Managers also maintain wildlife clearings, which are created through timber harvest or management of previously occurring fields, planted with grasses or legumes, and maintained through subsequent mowing or burning (Fig. 1D). Wildlife clearings are maintained to improve habitat quality for a suite of wildlife species, through increased herbaceous vegetation and the creation of forest edge (Healy and Nenno, 1983; Menzel et al., 1999; Ricks et al., 2016; Stewart et al., 2000).

Private land use patterns also act to mimic some historical landscape drivers, namely grazers, in the form of small-scale cattle and hay production. Modern pastures do not reflect the pre-settlement flora and fauna of Appalachian grasslands, however these areas do maintain openings that contain herbaceous vegetation and dense understory cover in surrounding forest edges. It is important to consider that in the predominately forested landscape of the Appalachians, these private fields maintained through mowing and grazing compose the majority of open habitat.

These shifts in Appalachian forest structure and composition, and the management efforts to restore disturbance regimes, have considerable implications for native wildlife (Litvaitis, 2001). However, empirical investigations of relationships between wildlife and forest disturbance are scarce, especially regarding carnivores. Bobcats (*Lynx rufus*) are a fitting species to examine the effects of forest disturbance on wildlife. Bobcats are ambush predators and obligate carnivores, thus in forested ecosystems, they select for densely vegetated understories that provide concealment cover and areas of abundant prey (Godbois et al., 2004; Kolowski and Woolf, 2002, Litvaitis et al., 1986; Tucker et al., 2008). Due to the aforementioned forest trends, the dense understory that bobcats presumably select is increasingly scarce in forested areas of the Appalachians in which disturbance regimes remain altered. The open canopy and resulting dense understory of pre-settlement Appalachian forests was likely much better suited to the foraging ecology of bobcats. The even-aged regeneration and mesophication of modern Appalachian forests have resulted in a heavily-shaded forest interior. These landscape patterns also have implications for bobcat prey. Suitable early successional habitat for common bobcat prey species is decreasing throughout much of the eastern United States (Litvaitis, 2001). Tree squirrels (*Sciurus* spp.), which are common bobcat diet items in the Appalachians (Morin et al., 2016, Progulske, 1955), are highly dependent on oak mast (Short, 1976). As carnivores, bobcats are closely tied to their prey, which are heavily influenced by forest management (Conner and Leopold, 1996).

Managers require information on local wildlife species and ecological processes when planning land management strategies. As one of the largest predators in Appalachian ecosystems, and the only extant native felid species in the region, bobcats are a species worthy of consideration when planning habitat management actions. We conducted this study in a site comprised of conditions representative of the majority of the Valley and Ridge province of the Appalachians and areas where managers conduct efforts to restore Appalachian mixed-oak ecosystems and enhance wildlife habitat through disturbance, specifically timber harvest, maintained clearings, and reintroduction of fire. As an obligate carnivore with a diverse diet, bobcats can serve as a surrogate species, indicating the response of a broader faunal community to management actions. We used resource selection analysis to investigate how bobcats respond to timber harvest, maintained clearings, and prescribed fire on a landscape otherwise dominated by closed-canopy forest. We predicted that bobcats would select areas of timber harvest, forest edge, and prescribed fire, and avoid areas of forest interior.

2. Methods

2.1. Study area

The study area encompasses the western half of Bath County, Virginia, adjacent to the border with West Virginia (Fig. 2).

Bath County is located in the Valley and Ridge physiographic province of the Appalachian Mountain range, characterized by long, parallel ridges with narrow valleys. Elevation ranges from 343 m to 1363 m. Temperature ranges from a mean minimum temperature of −4.6C in January to a mean maximum temperature of 31.6C in July (National Oceanic and Atmospheric Administration, public data 2012). Average annual precipitation is 97.8 cm (National Oceanic and Atmospheric Administration, public data 2012). The forest structure primarily consists of mature deciduous forest, with common overstory species including oak, hickory (*Carya* spp.), maple (*Acer* spp.), and tulip poplar (*Liriodendron tulipifera*). Evergreen conifers are present in some forest stands, with common overstory species including pines (*Pinus* spp.) and hemlock (*Tsuga* spp.). Common midstory and understory species include rhododendron (*Rhododendron* spp.), flowering dogwood (*Cornus florida*), sassafras (*Sassafras albidum*), eastern redbud (*Cercis canadensis*), striped maple (*Acer pensylvanicum*), viburnum (*Viburnum* spp.), witch hazel (*Hamamelis virginiana*), mountain laurel (*Kalmia latifolia*), blueberry (*Vaccinium* spp.), multiflora rose (*Rosa multiflora*), raspberry and wineberry (*Rubus* spp.), common greenbrier (*Smilax* spp.), and a wide diversity of herbaceous groundcover including ferns. Other than bobcats, the carnivore guild includes coyotes (*Canis latrans*), black bears (*Ursus americanus*), and a diverse group of smaller carnivores. Common bobcat diet items are squirrels (*Sciurus* spp.), voles (*Microtus* spp., *Myodes gapperi*), mice (*Peromyscus* spp.), cottontail rabbits (*Sylvilagus* spp.), and white-tailed deer (*Odocoileus virginianus*; Morin et al. (2016)). Bath County exemplifies the forest-dominated landscape of the Valley and Ridge Appalachians, with public, forested land on the steep ridges, and narrow strips of private, low intensity development and agriculture in the flatter valley bottoms. Bath County is 90% forested land cover, much of which consists of contiguous swaths of forest managed by government agencies. Within the study area, 52% of the land is the George Washington National Forest (GWNF), 9% is state managed Wildlife Management Area and State Park land, and 4% is land owned and managed by The Nature Conservancy (TNC).

The use of prescribed fire is relatively widespread in the study area compared to surrounding areas of the Appalachians. The average burn unit size in our study area was 676 ± 104 ha ($\bar{x}$ ± SE), but since many units are adjacent, they are sometimes burned simultaneously. Burns were typically conducted during the late dormant season or early growing season (February-May). Smaller burns were hand-ignited and larger burns (> 500 ha) were ignited with a combination of hand and aerial-ignition (Lorber et al., 2018). The average size of forest stands harvested within the previous 15 years was 8 ± 0.5 ha ($\bar{x}$ ± SE). Timber harvest occurred in these stands as recently as 1 year prior to the study. Timber harvest prescriptions varied, with approximately 15% of stands clearcut and the remainder consisting of various shelterwood prescriptions.

2.2. Bobcat capture and handling

We captured bobcats using cage traps (Camtrip Cages, Bartsow, California, USA and Briarpatch Cages, Rigby, Idaho, USA) in accordance with Virginia Tech IACUC protocol #16-071. We checked traps twice daily (morning and afternoon). We immobilized bobcats with a mixture of 10–15 mg/kg ketamine hydrochloride and 1 mg/kg xylazine using hand injection with syringe. We monitored and recorded respiratory rates, heart rates, and temperatures every 10 min. We used tooth growth and condition, body morphology, and teat/scrotum characteristics to determine whether bobcats were juvenile or adult (Jackson et al., 1988). We fitted adult bobcats with Iridium GPS collars (Advanced Telemetry Systems, Isanti, Minnesota, USA). All bobcats captured were marked with color-coded numbered ear tags. Following handling, we reversed xylazine with 0.125 mg/kg yohimbine, administered either rectally or intramuscularly, and allowed bobcats to recover in the cage trap for 30 min to 1 h before release. We programmed GPS collars to record locations at 2 and 4-hour intervals, but subsampled all data to a 4-hour fix rate for these analyses.

2.3. Characterizing forest disturbance

We characterized relevant habitat variables using geographic information system (GIS) data from a variety of sources. We acquired land cover data from the Virginia Geographic Information Network, which classifies land cover into 11 categories (Appendix A), 6 of which (forest, scrub/shrub, harvested/disturbed, turfgrass, pasture, and cropland) we used in the development of our covariates. Prescribed fire data included results from an analysis on the effects of prescribed fire on forest canopy structure conducted by USFS and TNC, in which leaf-on, 1 m-resolution aerial imagery was used to digitize canopy openings created by prescribed fire treatments in the GWNF (Lorber et al., 2018). Timber harvest and wildlife clearing data were acquired from USFS and Virginia Department of Game and Inland Fisheries (VDGIF).

To characterize edge effects around forest openings, we aggregated data from all sources into two types of openings - maintained fields and disturbed forest. The "fields" class of opening consisted of combined turf, pasture, and crops land cover classes, and all wildlife clearings. The "disturbed" class of opening consisted of shrub/scrub and harvested/disturbed land cover classes, all timber harvest within 15 years, and canopy openings resulting from fire. We then classified forest edge as the interface between these openings and forest land cover, and classified it as either forest-field edge or forest-disturbed edge, depending on which type of opening was adjacent to the forest edge. We delineated between forest edge along open fields and regenerating, young forest due to structural differences between the hard and soft edges, respectively. We characterized forest interior as forest that is ≥ 300 m from contrasting land cover types, since forest edge can influence primary forest processes up to a distance of approximately 300 m (Harper et al., 2005). We characterized fire-created canopy openings using results from the analysis on effects of prescribed fire on forest canopy structure conducted by USFS and TNC (Lorber et al., 2018), which included all forest with less than 50% canopy cover as a result of fire. In our study area, the earliest of these prescribed fire treatments was conducted 14 years prior to our study, but the majority were conducted within the previous 5 years, and the most recent large fires outside of the burn units likely occurred a century or longer ago. We characterized timber harvest by combining all stands harvested within the past 15 years, as 1–15 year old stands are typically characterized by seedling-sapling structure (Lorimer and White 2003). The majority of these stands were harvested within 5 years of the study (52%), and only 20% were harvested 10–15 years prior to the study. We initially planned to delineate timber harvest by harvest prescription (i.e. shelterwood vs. clearcut) and time since harvest. However, due to the small sample size of bobcat home ranges that overlap differing prescriptions and/or ages of harvested stands, we combined all types and ages of cuts. Despite some variation among these harvested stands, our primary goal was to capture the more drastic differences between recently harvested stands and the surrounding, undisturbed forest. Lastly, we created distance raster layers by calculating Euclidean distance to each of these variables. The 5 resulting covariates were distance to forest-field edge, distance to forest-disturbed edge, distance to forest interior, distance to fire-created canopy openings, and distance to timber harvest. We used distance-based covariates to facilitate model interpretation, reduce the influence of telemetry error, and because the effects of the focal landscape processes can extend beyond their boundaries.

2.4. Resource selection analysis

Due to the spatial organization of bobcat home ranges in relation to burned and harvested forest stands, we removed certain individuals from analyses examining effects of fire or timber harvest, and modeled these effects separately. Since we used distance-based analyses and not a categorical approach, we removed from analyses bobcats that exceeded a maximum distance from these areas, instead of simply removing individuals with home ranges that did not overlap areas of prescribed fire or timber harvest. The effects of a disturbed area can reach beyond its boundaries through edge effects and, across an even broader area, increased bobcat prey availability, since movements of prey can be influenced by these disturbed areas. For example, Cherry et al. (2018) found that white-tailed deer are attracted to recently burned areas, but maintain unburned portions of their home ranges, increasing movement rates to access the burned areas. Based on ranging behavior of one of the most mobile bobcat diet items, white-tailed deer, we infer that bobcats could benefit from increased prey availability resulting from prescribed fire and timber harvest within an area comparable to a deer home range. Estimated seasonal home range size of white-tailed deer in a nearby and ecologically similar area in West Virginia, when averaged across sex and seasons, was approximately 1 km^2 (Campbell et al., 2004). Therefore, if a bobcat's closest location to timber harvest or fire created canopy openings exceeded 1 km in distance, we excluded that bobcat from analyses that included those covariates.

We developed resource selection functions (RSFs) to examine 3rd order (within home range) bobcat resource selection (Johnson 1980), in a use-availability framework using a generalized linear mixed model in the Program R package lme4 (Bates et al., 2015). We defined resource availability within a 95% minimum convex polygon (MCP) around each bobcat's locations. Within each individual's MCP, 10 simulated locations for each real location were randomly placed to sample available habitat, resulting in 789 ± 122 ($\bar{x}$ ± SE) simulated locations per km^2. We then extracted the value of all covariates at each real and simulated location. No covariates within models were highly correlated (all covariates had $r < |0.45|$; Pearson's correlation). The binary response variable was whether a location was used or available (used = 1, available = 0). Predictor variables included distances to 5 habitat features: forest-field edge, forest-disturbed edge, fire-created canopy openings, forest stands harvested within 15 years, and forest interior. We fit 3 separate models examining the effects of forest structure and disturbance. Due to the spatial arrangement of disturbance treatments relative to bobcat home ranges, we subset our data to only include bobcats we assumed could interact with those treatments. Our first model (Model A) included all bobcats and examined selection of forest interior, forest-field edge, and forest-disturbed edge. Our second model (Model B) only included bobcats that experienced fire treatments, thus we added the distance to fire-created canopy openings covariate. Our third model (Model C) only included bobcats that experienced timber harvest treatments, thus we added the distance to timber harvest covariate. The distance to forest-disturbed edge covariate was not included in models B or C, because areas of prescribed fire and timber harvest composed most of the "disturbed" class of opening. We scaled and centered all predictor variables, to reduce model convergence issues. We included random intercepts for individual bobcats (Gillies et al., 2006). We evaluated selection or avoidance based on whether or not a coefficient significantly differed from zero ($\alpha = 0.05$). We inferred habitat selection if used points were closer to habitat variables than random locations, and avoidance if used points were further from habitat variables than random locations. Each model contained 3 covariates (see Table 2) and we compared coefficient estimates within models, from largest to smallest, to evaluate relative importance of the various covariates.

2.5. Resource use

We also calculated the number of bobcat locations within areas of timber harvest, fire-created canopy openings, fields, forest-field edge, forest-disturbed edge, and forest interior. We calculated use in addition to distance-based resource selection to determine the extent bobcats were actually within boundaries of each area versus using locations closer to these areas, but not within their boundaries. Timber harvest, fire-created canopy openings, and forest interior were identical to covariates used in RSFs. Although a linear edge was used in RSFs (due to use of distance-based covariates), we used a 300 m buffer to calculate number of locations within forest-field edge and forest-disturbed edge. Fields were characterized using the same data used to create the forest-field edge (see Characterizing Forest Disturbance).

3. Results

We captured 10 bobcats from January - April 2018, excluding 1 from analysis due to < 1 month of monitoring, resulting in a dataset of 9 bobcats (6 males, 3 females). Length of collar deployments ranged from 12 to 56 weeks (Table 1).

Table 1
Duration of collar deployments and months monitored for each of 9 collared bobcats in Bath County, Virginia in years 2018–2019.

Bobcat ID	Weeks Deployed	Months Monitored
F12	12	Jan 2018–Apr 2018
M13	54	Feb 2018–Feb 2019
M15	36	Feb 2018–Oct 2018
M16	56	Mar 2018–Mar 2019
F18	22	Mar 2018–Jul 2018
F20	52	Apr 2018–Mar 2019
M21	52	Apr 2018–Mar 2019
M22	25	Apr 2018–Oct 2018
M23	51	Apr 2018–Apr 2019

Table 2
Model results for resource selection functions for 9 bobcats collared in Bath County, Virginia in years 2018–2019, including separate models for various covariate combinations. Models are binomial generalized linear mixed-effects models. Results include β coefficients (β), and standard errors (SE), z values, and p values from Wald tests.

Model	Covariate	β	SE	Z value	P value
A) *All individuals*	disturbed edge[a]	−0.236	0.014	−16.387	< 0.001
n = 9 (6 male, 3 female)	field edge[b]	−0.175	0.012	−14.310	< 0.001
	forest interior[c]	0.078	0.011	7.200	< 0.001
B) *Individuals within 1 km of fire*					
n = 8 (5 male, 3 female)	fire[d]	−0.327	0.017	−19.192	< 0.001
	field edge	−0.186	0.013	−14.397	< 0.001
	forest interior	0.051	0.012	4.374	< 0.001
C) *Individuals within 1 km of timber harvest*					
n = 7 (5 male, 2 female)	timber[e]	−0.060	0.015	−4.127	< 0.001
	field edge	−0.265	0.015	−18.158	< 0.001
	forest interior	0.145	0.012	12.092	< 0.001

[a] The "disturbed edge" covariate is the distance to forest edge along combined shrub/scrub and harvested/disturbed land cover classes, all timber harvest within15 years, and canopy openings resulting from fire.
[b] The "field edge" covariate is the distance to forest edge along combined turf, pasture, and crops land cover classes, and all wildlife clearings.
[c] The "forest interior" covariate is the distance to forest that is 300 m or further from contrasting land cover types.
[d] The "fire" covariate is the distance to open canopy structure resulting from prescribed fire.
[e] The "timber harvest" covariate is the distance to all timber harvest on public lands within 15 years.

Our results provide evidence for selection of locations within home ranges that are closer to forest-field edge, forest-disturbed edge, fire-created canopy openings, harvested forest stands, and farther from forest interior than would be expected at random (Table 2, Fig. 3).

Avoidance of forest interior by bobcats was supported by all 3 models (Table 2, Fig. 3). The model including all individuals (model A, n = 9) showed stronger selection for closer distances to forest-disturbed edge ($\beta = -0.281$, SE = 0.013) than for distance to forest-field edge ($\beta = -0.159$, SE = 0.011). The model investigating the effects of fire on resource selection (model B, n = 8), showed stronger selection for closer distances to fire-created canopy openings ($\beta = -0.321$, SE = 0.015) than forest-field edge ($\beta = -0.171$, SE = 0.011). Lastly, the model investigating the effects of timber harvest on resource selection (model C, n = 7), showed stronger selection for closer distances to forest-field edge ($\beta = -0.229$, SE = 0.013) than timber harvest ($\beta = -0.062$, SE = 0.013).

Resource use data show that bobcats use the interior of fire-created canopy openings, areas of timber harvest, or fields, less frequently than the forest edge surrounding these areas (Table 3). The number of locations actually within disturbed areas was extremely low in some cases. However, most locations were in forest edge immediately surrounding (< 300 m) these disturbed areas, for multiple bobcats. It is also important to note that disturbed areas were not within home range boundaries for some bobcats.

4. Discussion

Variation in availability of prey likely drives many of the resource selection patterns observed in bobcats (Conner and Leopold 1996, Godbois et al., 2004, Litvaitis et al., 1986). As obligate carnivores, bobcats must acquire sufficient prey to meet energetic requirements necessary to survive and reproduce, yet as ambush predators they also require sufficient concealment cover to access available prey. Prescribed fire, timber harvest, and edge effects are all mechanisms that can increase prey and concealment cover on the landscape (Harper et al., 2016, Jorge et al., 2020, Litvaitis, 2001, Masters et al., 1993, Williamson and Hirth, 1985). The selection for locations closer to prescribed fire, timber harvest, and forest edge that we observed for bobcats in this study most likely reflect utilization of increased prey and also concealment cover resulting from these mechanisms.

Bobcats strongly selected for canopy openings resulting from prescribed fire. While all canopy openings and forest edges allow increased sunlight to reach the forest floor and spur understory growth, whether created from fire, timber harvest, or maintained clearings, prescribed fire can influence the ecosystem in other unique and complex ways. For years after a fire event, soil nutrients can continually increase due to the gradual sequestration of charcoal and growth of post-fire, nitrogen-fixing vegetation (Certini, 2005, Johnson and Curtis, 2001). Fire can also benefit the growth of fire-adapted tree species, such as oaks, which provide forage in the form of mast for bobcat prey species like deer and squirrels, while inhibiting the success of mesophytic tree species such as maples (Brose et al., 2013, Nowacki and Abrams, 2008). Delayed mortality of overstory trees can occur as late as 5 years following a fire (Yaussy and Waldrop, 2010). Until recently, much of the prescribed fire research and management has been silviculturally targeted, leading to a focus on low-severity fires that minimize canopy mortality (Lorber et al., 2018). Recent research has found that a variety of wildlife species in the Appalachians respond positively to prescribed fire treatments, however much of these positive responses are due to indirect effects on habitat resulting from canopy mortality (Harper et al., 2016, Klaus et al., 2010, Rush et al., 2012). Little et al. (2018) found no effect of time-since-fire on bobcat habitat use in a longleaf pine (*Pinus palustris*) savanna, which may be due to the nature of fire prescriptions used at that site. The fires in their study area were often small scale (< 40 ha mean patch size burned), low-severity, and lacked topographically-mediated heterogenity in fire severity. In contrast, the fires in our study area typically occur over a much wider area (> 500 ha) of rugged and varied topography, leading to mixed-severity fires with greater canopy mortality. By explicitly focusing on open canopy structure created by fire, we were able to examine bobcat selection for these areas specifically. Our work builds on knowledge that prescribed fire can benefit wildlife, and specifically adds to the understanding that canopy mortality resulting from mixed-severity burns is an important component for some species.

Bobcats selected for areas of recent timber harvest, which has been observed in previous studies, although few studies have explicitly examined the influence of timber harvest on bobcat habitat use. In Mississippi, bobcats were found to select young pine forests (Chamberlain et al., 2003, Conner and Leopold, 1996). In contrast, Little et al. (2018) found that bobcats avoided young pines in southwestern Georgia, which they attributed to a lack of herbaceous cover and low small mammal abundance in those areas. Small mammal activity and abundance has been found to be higher at areas disturbed by timber harvest in the Appalachians (Kaminski et al., 2007), which may partially explain the selection for these areas by bobcats in our study area.

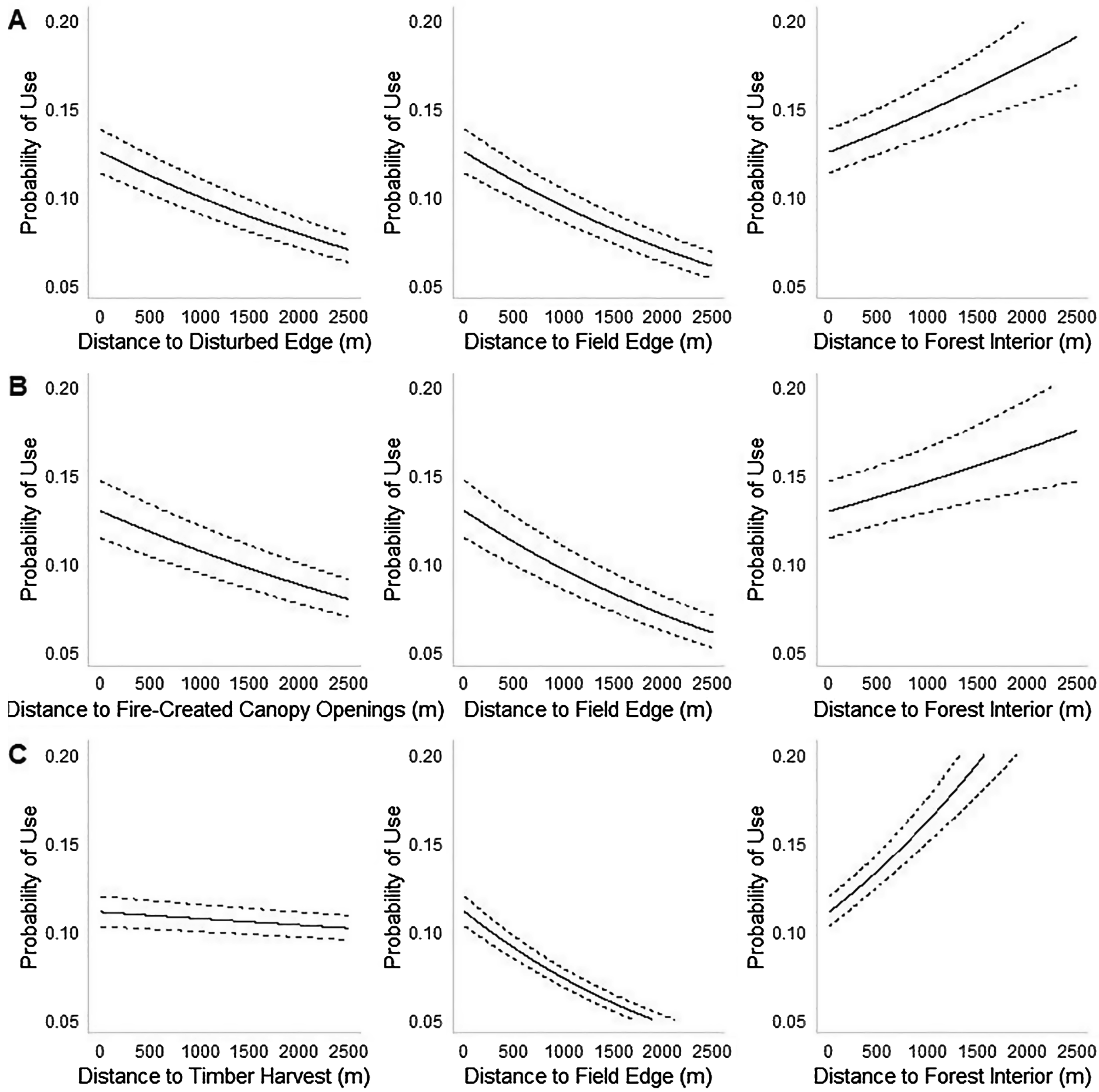

Fig. 3. Effects of distance to forest edge along fields, distance to forest edge along disturbed forest, distance to canopy openings resulting from fire, distance to timber harvest, and distance to forest interior (with 95% confidence intervals) on relative probability of bobcat use in Bath County, Virginia, in 2018–2019. Results are from 3 separate 3rd order resource selection functions including all individuals (n = 9, Model A), only individuals within 1 km of fire-created canopy openings (n = 8, Model B), and only individuals within 1 km of timber harvest (n = 7, Model C).

Although we observed bobcat selection of recently harvested forest, this selection was relatively weak compared to forest-field edge, and selection for areas of fire created canopy openings was even stronger than forest-field edge. These differences in selection strength may relate to the size, shape, and composition of the canopy openings resulting from fire versus timber harvest. Compared to the irregularly-shaped and clumped canopy openings created by prescribed fire, timber harvest operations in the study area typically have a more linear edge and are farther apart, which may be largely attributed to the logistical constraints of planning and executing timber harvests in mountainous terrain. Conversely, large fire treatments can be executed via helicopter ignition and spread across a topographical gradient. The resulting "patchy" distribution of canopy openings can then influence processes along an entire mountainside. Based on this, we expect prescribed fires to have more broad-scale impacts on landscape patterns, whereas the impacts of timber harvest may be more localized. Importantly, timber harvest can be an essential tool for opening canopy in conjunction with fire, particularly in areas where mid to high-intensity fires may not be feasible, and thus can be used with prescribed fire to create and enhance wildlife habitat (Brose and Van Lear 1998, Harper et al., 2016).

Bobcats avoided forest interior, and selected forested edges with stronger selection for edges associated with disturbed forest than fields. Bobcats are known to select for dense vegetative cover (Kolowski and Woolf 2002), which is likely far more prevalent along forest edge than the heavily-shaded interior. In a study examining small mammal communities across a gradient from wildlife openings to forest interior in the southern Appalachian Mountains, Menzel et al. (1999) captured over 3 times as many mice (*Peromyscus* spp.) as red-backed voles (*Clethrionomys gapperi*), but found that voles were most abundant in forest edge, whereas mice were most abundant in forest interior. Voles occur twice as

Table 3
Bobcat resource use of fire-created canopy openings, areas of timber harvest, fields, forest-field edge, forest-disturbed edge, and forest interior, for 9 bobcats collared in Bath County, Virginia in years 2018–2019. Shown are number of bobcat locations for each resource type and percentage of locations in each resource type out of total locations included in parentheses. Although bobcats were closer to disturbed areas than expected, use was concentrated in the forest edges resulting from these areas rather than within them.

Bobcat	fire	timber	field	field edge	disturbed edge	forest interior
F12	54 (15)	14 (4)	2 (1)	144 (41)	93 (26)	37 (11)
F18	0 (0)	1 (< 1)	10 (2)	163 (30)	3 (1)	343 (62)
F20	37 (3)	0 (0)	6 (1)	248 (22)	207 (18)	538 (47)
M13	0 (0)	0 (0)	49 (2)	555 (28)	55 (3)	1119 (57)
M15	0 (0)	8 (1)	17 (2)	461 (41)	16 (1)	239 (21)
M16	117 (7)	0 (0)	0 (0)	281 (16)	757 (43)	412 (23)
M21	94 (5)	0 (0)	81 (5)	771 (44)	316 (18)	160 (9)
M22	20 (2)	1 (< 1)	27 (3)	404 (46)	188 (22)	127 (15)
M23	250 (14)	0 (0)	46 (3)	488 (27)	438 (24)	422 (23)
Mean	64 (5)	3 (1)	26 (2)	389(33)	230 (17)	377 (30)

frequently as mice in bobcat diets in western Virginia (Morin et al., 2016), which may reflect use of forest edge as foraging areas by bobcats, due to increased availability of voles. Despite a higher abundance of mice in the forest interior, the lack of dense understory likely decreases their availability to bobcats due to reduced concealment cover needed to stalk and ambush prey. Bobcat selection for multiple types of edge highlights the importance of edge habitat in this forest-dominated system. Our resource use data show that although bobcats were closer to areas of disturbance than expected, it is the forest edges resulting from these areas that are actually most important. Our findings build on previous research that has found bobcat selection for forest edge (Abouelezz et al., 2018, Reed et al., 2017), and suggest that bobcats may be edge specialists in forested ecosystems. The difference in selection among edge types may reflect selection for the structure of soft edges along a mature forest – disturbed forest gradient versus the hard forest edges along fields. Another consideration is potential increased risk exposure along field edges, most of which are privately owned, as the most common source of bobcat mortality in our study area was hunting and trapping near these areas. Despite these considerations, forest edge along fields likely composes the majority of suitable bobcat habitat within the region, as young forest is far less common than fields

By conducting this research in a study area with comparatively frequent and widespread use of prescribed fire, we have gained novel insight into the effects of fire on bobcat space use, particularly in the forests of the Appalachians. A limitation of this study was the relatively small sample size of bobcats. Further, the spatial distribution of bobcats in relation to the focal processes hindered a direct comparison of prescribed fire and timber harvest. Nonetheless, our findings that bobcats exhibited stronger selection for areas of prescribed fire than forest edge, but selected forest edge more strongly than timber harvest, suggests that prescribed fire may yield a stronger influence on bobcat habitat use. A larger sample size of bobcats covering a wider range of timber harvest prescriptions and stand ages would allow a more in-depth analysis of the effects of timber harvest on bobcat space use. Thus, future studies investigating the effects of timber harvest on bobcat space use should examine a range of harvest prescriptions and stand ages.

5. Management implications

Land managers in the Appalachians use timber harvest and, to a lesser extent, prescribed fire as the primary mechanisms to create young forest to benefit wildlife species. In our study area, prescribed fire has outpaced recent timber harvest in acreage, enabling a view into potential future management efforts in the region. As the use of prescribed fire increases, we recommend that managers consider our findings when planning future efforts and communicating them to the public. Creation of open canopy structure is one aspect of prescribed fire that is explicitly and quantitatively outlined in the GWNF management plans, which state goal percentages of burn areas to convert to open canopy and early successional vegetation. In these management plans, goals for creating open canopy structure suggest management for a particular suite of wildlife species, including both game (e.g. deer and wild turkey [*Meleagris gallopavo*]) and nongame species (e.g. songbirds and reptiles; Harper et al., 2016, Lorber et al., 2018). Our finding that bobcats select for canopy openings resulting from prescribed fire supports previous findings that this practice is an effective wildlife management tool (Harper et al., 2016). We suggest managers conduct mixed-severity burns, and use timber harvest in conjunction with fire, to mimic historic disturbance regimes and create uneven-aged stands that both restore pre-settlement forest structure and enhance wildlife habitat. If managers are interested in using disturbance specifically to the benefit of certain common bobcat prey species, they might aim for a higher percentage of canopy openings or wider distribution of canopy openings, to avoid attracting bobcats and their prey to the same localized areas.

Public perception of habitat management strategies, particularly timber harvest, can be negative. It is likely that much of the general public does not understand the altered state of forest ecosystems in eastern North America. The dissemination of information regarding the ecological benefits of prescribed fire and timber harvest can improve public perception of these practices (Cortner et al., 1990, Kearney 2001). Much of the public communication regarding these management strategies is currently focused on certain migratory bird species (e.g. golden-winged warbler [*Vermivora chrysoptera*]) or popular game species (e.g. white-tailed deer), which caters to specific stakeholders (e.g. birders and hunters). Bobcats are a charismatic species that is widely recognized and generally appreciated by the broader public. We recommend that managers explicitly reference bobcat ecology, perhaps even using them as a flagship species, when communicating to the public regarding efforts to improve habitat through prescribed fire and timber harvest.

Habitat quality is a crucial component of bobcat management, which is evidenced by the current distribution of bobcats, as the areas where bobcats remain extirpated or at low abundance are primarily monoculture-dominated landscapes such as the Midwest or Delmarva Peninsula (Roberts and Crimmins 2010). The importance of forested habitat to bobcats in eastern North America has been shown repeatedly in past research (Abouelezz et al., 2018, Donovan et al., 2011, Lovallo and Anderson, 1996, Tucker et al., 2008). Our findings highlight that future research and management efforts should also consider the importance of forest structure and composition.

CRediT authorship contribution statement

David C. McNitt: Conceptualization, Investigation, Methodology, Formal analysis, Data curation, Writing - original draft, Visualization, Project administration. **Robert S. Alonso:** Investigation, Methodology, Resources, Writing - review & editing, Project administration, Conceptualization. **Michael J. Cherry:** Conceptualization, Methodology, Writing - review & editing. **Michael L. Fies:** Writing - review & editing, Project administration, Funding acquisition, Resources, Conceptualization, Supervision. **Marcella J. Kelly:** Writing - review & editing, Project administration, Funding acquisition, Resources, Conceptualization, Supervision, Investigation, Methodology.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. All land cover categories composing the Virginia geographic information network (VGIN) Virginia land cover Product. The 1 m resolution dataset is based upon 2011–2014 4-band orthophotography.

11 - Open Water	Drainage network and basins such as rivers, streams, lakes, canals, waterways, reservoirs, ponds, bays, estuaries, and ocean as defined by the National Hydrography Dataset
21 - Extracted Impervious	Areas characterized by a high percentage of constructed materials such as asphalt and concrete, buildings and parking lots, and infrastructure as defined by the Environmental Protection Agency (EPA), that extends beyond local planimetric data provided.
22 - External Impervious	Locally maintained planimetric data such as buildings, parking lots, edge of pavement, roads, and any other paved surface data.
31 - Barren	Areas with little or no vegetation characterized by bedrock, desert pavement, beach and other sand/rock/clay accumulations, as well as areas of extractive mining activities with significant surface expression as defined by the EPA.
41 - Forest	Areas characterized by tree cover of natural or semi-natural woody vegetation as defined by the EPA, encompassing an acre in size; this class includes deciduous, evergreen, and mixed foliage types
42 - Tree	Characterized by tree cover of natural or semi-natural woody vegetation as defined by the EPA, that does not encompass at least an acre in size; this class includes deciduous, evergreen, and mixed foliage types.
51 - Scrub/Shrub	Areas characterized by natural or semi-natural woody vegetation with aerial stems generally less than 6 m tall; features classified here will include those that would otherwise be determined Harvested/Disturbed but appear to show unmanaged stunted growth, or managed as easements.
61 - Harvested/Disturbed	Areas of forest clear-cut, temporary clearing of vegetation, and other dynamically changing land cover due to land use activities as defined by the EPA; these features should be categorized only where there is 30% canopy cover or less.
71 - TurfGrass	Primarily grasses; including vegetation planted in developed settings for erosion control or aesthetic purposes, as well as natural herbaceous vegetation and undeveloped land, including upland grasses and forbs, as defined by the EPA.
81 - Pasture	Areas of grasses, legumes, or grass-legume mixtures planted for livestock grazing or the production of seed or hay crops as defined by the EPA.
82 - Cropland	Characterized by herbaceous vegetation that has been planted or is intensively managed for the production of food, feed, or fiber, or is maintained in developed settings for specific purposes as defined by the EPA.
91 - NWI/Other	Areas where forest, shrubland vegetation, or perennial vegetation accounts for 25% to 100% of the cover and the soil or substrate is periodically saturated with or covered with water. This class has an additional attributed subclass to correspond with the extracted software output had external wetland data not been incorporated.

Appendix B. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118066.

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