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ORIGINAL RESEARCH

# Determining puma habitat suitability in the Eastern USA

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**Abstract**
Pumas (*Puma concolor*) were eliminated from most of the eastern USA a century ago. In the past couple of decades, their recovery in the West has increased puma dispersal into the Midwest, with some individuals even traveling to the East Coast. We combined published expert opinion data and a habitat suitability index in an analysis that identified 17 areas in the Upper Midwest, Ozarks, Appalachia, and New England that could potentially host puma populations in the future. Thirteen of these were larger than 10,000 km$^2$ and so likely to ensure a puma population's long-term genetic health. Further, we quantified patch size, human density, livestock density, percent public land, and a sociocultural index reflecting wildlife values for comparing patches, as well as present a summary of current legislation relevant to puma management in the East. Our work may be useful in identifying suitable areas to restore pumas based not only on the quality of their biophysical habitat, but also on social values conducive to puma-human coexistence.

**Keywords** Habitat connectivity · Habitat suitability · Landscape connectivity · *Puma concolor* · Range expansion · Recolonize

## Introduction

One hundred fifty years ago, pumas (*Puma concolor*), also called cougars, mountain lions, and Florida panthers, roamed nearly every habitat in the Americas from the East to West coast and southern Canada to Chile (Culver et al. 2000; McCollough 2011). However, when European settlers spread across North America, they viewed carnivores as competitors for game, livestock and other resources (Gill 2010). As a result, they conducted wide-scale carnivore eradication efforts (Danz 1999). Early settlers also practiced unrestricted resource extraction, resulting in deforestation and precipitous declines

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of ungulate prey that supported large carnivores (Gill 2010). With the establishment of an independent USA, these practices evolved into federal and state bounty programs by the late 19th century, incentivizing the removal of pumas and other carnivores (Feldman 2007; Gill 2010). By the early 1900s, pumas were functionally extinct in the eastern two-thirds of the country, except southern Florida (Culver et al. 2000; McCollough 2011).

In the early 20th century, the USA transformed its wildlife management to restrict hunting and protect game species humans valued, which serendipitously protected the prey species needed to recover large carnivore populations as well (Gill 2010). In the 1970s, people increasingly perceived carnivores as important components of ecosystems, and pumas were given some level of protection across most of the West (Mattson and Clark 2010; Pritchard 2021). Since that time, western puma populations have recovered remarkably. Though pumas in the east are the same subspecies as those found in western North America (Culver et al. 2000), these protections did not have the same effect on eastern populations. The largest block of historic puma range in all the Americas that does not currently support breeding puma populations comprises the Midwest and Eastern USA (Nielsen et al. 2017; Fig. 1).

Since pumas have been extirpated from much of their previous distribution, they have been unable to perform important functions that contribute to ecological resilience (Barry et al. 2019; LaBarge et al. 2022). In addition, the absence of pumas has consequences for human health and wellbeing as well. For example, pumas mitigate human-deer collisions on roadways, saving human lives and millions of dollars in costs (Gilbert et al. 2021). There is also evidence that suggests pumas help control chronic wasting disease (Baune et al. 2021), which poses great concern for wildlife agencies and hunting communities. Reestablishing pumas in currently unoccupied habitat could help restore these important ecological relationships.

Early stages of puma recolonization have been documented in the Midwest and central-southern Canada (LaRue et al. 2012; LaRue and Nielson 2011; Glick 2014; O′Neil et al. 2014; Smith et al. 2016; Gantchoff et al. 2021; LaRue et al. 2022), spurring considerable research aimed at predicting how pumas will navigate current landscapes and where they may occur in the future (LaRue and Nielsen 2008). Pumas exhibit male-biased dispersal patterns in which males disperse greater distances than females (Sweanor et al. 2000), and therefore we expect males to appear in the East well before females (LaRue et al. 2012). For example, one young male puma dispersed from the Black Hills in South Dakota approximately 1800 miles to Connecticut, where he was killed on a highway in 2011 (Hawley et al. 2016). Several reports and papers have also explored the potential for reintroducing pumas in the East, as a conservation restoration strategy to expedite recolonization of former range (Brocke 1981; Laundre 2013).

Given the density of people and human infrastructure in the East relative to the West, an important next step in managing recolonizing carnivores is determining whether they can maintain viable populations on their own. Identifying potential habitat blocks that may host pumas in the future may also be useful in targeting proactive conflict mitigation strategies and other educational campaigns that support human coexistence with large carnivores.

Here, we combine expert opinion published in peer-reviewed literature (LaRue and Nielsen 2008) and a habitat suitability index to identify habitat patches where pumas could potentially reestablish locally self-sustaining populations in the East, without relying on dispersal and genetic rescue from nearby populations (i.e., metapopulation dynamics; Sweanor et al. 2000). The identified areas contain sufficient resources for supporting a long term puma population once established, independent of neighboring populations.


**Fig. 1** Current (shown in dark green) and historic (shown in dark green and light green combined) puma range. The largest unoccupied area, or the area with the largest opportunity for recolonization, is the eastern two-thirds of the USA. Figure adapted from IUCN Red List of Threatened Species: *Puma concolor*. (Color figure online)

## Materials and methods

### Study area

Our area of focus was the USA states bordering or east of the Mississippi River, and included Alabama, Arkansas, Connecticut, Delaware, District of Columbia, Florida, Georgia, Illinois, Indiana, Iowa, Kentucky, Louisiana, Maine, Maryland, Massachusetts, Michigan, Minnesota, Mississippi, Missouri, New Hampshire, New Jersey, New York, North Carolina, Ohio, Pennsylvania, Rhode Island, South Carolina, Tennessee, Vermont, Virginia, West Virginia, and Wisconsin. This large area was primarily composed of two ecoregions (EPA 2022), Eastern temperate forests and Northern forests, with a small portion of tropical wet forests in southern Florida. The climate, land use, habitats, and other landscape features were highly variable across this region. Regional climate ranged from continental, with cold or frigid winters and hot, humid summers; to humid subtropical, with mild winters and warm to hot and humid summers. Habitat types were similarly variable, from boreal forest and alpine regions in New England to tallgrass prairie and temperate deciduous forest in the Midwest to pond cypress swamp and pine savanna in the South.

### Identifying puma habitat patches

Pumas have been widely studied in the USA, which has provided a wealth of information on puma habitat requirements, including their selection preferences for vegetation types, human density, road proximity, livestock use, and snow depth (Table 1). We used expert opinion found in published scientific literature to identify several landscape dynamics that influence suitable puma habitat availability, puma habitat selection, as well as puma population viability. For example, pumas are ambush predators that require vegetative structure for cover, and therefore they select against open habitats (Gray et al. 2016). Pumas also select against areas of deep snow, likely because it hinders movement and reduces ungulate prey abundance (CDFW 2015; Laundré and Hernández 2003; Poole and Mowat 2005). Though not a wilderness obligate species, pumas also select against urban and suburban areas (Burdett et al. 2010; Wilmers et al. 2013; Yovovich et al. 2020). Pumas utilize fire roads, dirt roads, and other low-speed, low-use roadways, but their movement is limited by high-speed roadways, highways, and interstates (Dickson et al. 2005; Knopff et al. 2014; Wilmers et al. 2013). Conflict as a product of carnivore-livestock interactions is among the greatest threats to carnivores worldwide, and pumas are no exception (Ripple et al. 2014). Habitat with limited livestock may be more suitable puma habitat, because it reduces the risk of puma mortality via legal depredation permits or retaliatory killing (Guerisoli et al. 2021). We selected seven ecological and geographical variables that reflect puma habitat requirements and implemented a threshold approach to delineate areas of viable habitat for each variable (Table 1). We excluded all areas that did not meet our threshold requirements for all seven variables, and then combined connected habitat into patches for further analyses (for variable preprocessing and associated metadata, see supplemental material).

Based on research on puma genetic diversity, we applied two size thresholds to our resulting patches to identify best habitat for potential puma populations in the East (Dellinger et al. 2020). First, we excluded all areas less than 6,000 km$^2$, which some evidence suggests is the minimum area required to maintain sufficient puma genetic diversity to sustain long-term populations, and then a stricter 10,000 km$^2$ threshold, as this has been

**Table 1** Variable thresholds for puma habitat suitability to be applied to the East Coast, as defined by previous literature, and data sources used in the modeling analyses for predicting suitable patches for puma survival and persistence

| Ecological assumption | Habitat variable | Threshold description | Data source | Spatial resolution | Dates |
|---|---|---|---|---|---|
| Pumas select against open habitats in North America (LaRue and Nielsen 2008; Burdett et al. 2010; Gray et al. 2016) | Land cover | Exclude agriculture, high elevation rock and grasslands | Sulla-Menashe and Friedl (2018) | 500 m | 2019 |
| Pumas require structured habitat for hunting and survival (Gray et al. 2016) | Forest cover | Pumas excluded from cells with < 53% forest cover | Hansen et al. (2013) | 30 m | 2000—2020 |
| Pumas follow prey, and deer and elk avoid deep snow (Laundré and Hernández, 2003; Poole and Mowat, 2005) | Maximum snow depth | Pumas (and puma prey) excluded when average winter snow depth ≥ 50 cm | SNODAS | 1 km | 2010—2020 |
| Pumas excluded from areas with high housing density (Burdett et al. 2010) | Housing density | Pumas excluded when housing density ≥ 0.68 units/ha | ICLUS | 90 m | 2010 |
| Pumas excluded from habitat adjacent to people (Wilmers et al. 2013; Yovovich et al. 2021) | Human development proximity | Pumas excluded from habitat ≤ 600 m from human structures | Yang et al. (2018) | 30 m | 2016 |
| People excluded from habitat immediately adjacent to large highways (Knopff et al. 2014) | Highway proximity | Pumas excluded from habitat within 170 m of interstate highways and major arterials | TIGER US Census Roads | NA | 2016 |
| Pumas and livestock may have conflict that leads to lower puma survival; puma survival is higher in habitat with low livestock density (Guerisoli et al. 2021) | Livestock density | Pumas excluded from habitat with ≥ 14.5 animals/$km^2$ | Robinson et al. (2014) | 10 km | 2010 |

suggested by researchers as the size needed to ensure long-term genetic health (Dellinger et al. 2020). All spatial analyses were conducted using Google Earth Engine (Gorelick et al. 2017).

### Descriptive metrics for habitat patches

For all the patches that met either size threshold (i.e., > 6,000km$^2$ or > 10,000km$^2$), we created a suite of metrics across which we might compare them by (1) total patch area,(2) mean sociocultural index values based on county-level projections in Manfredo et al. (2021), (3) percentage of the patch that is public land (Conservation Biology Institute 2012), (4) mean human population density (GPWw4; CIESIN 2018), and (5) mean livestock density (Robinson et al. 2014). The sociocultural index values (Manfredo et al. 2021) range from 0 to 1, and reflect a breadth of perspectives on wildlife and natural resources, from domination, where wildlife are viewed primarily as resources for human consumption and benefit, to mutualism, where wildlife are viewed as part of one's social community, having rights like humans, and deserving of care and compassion. When compared with mutualists, those with a domination orientation are less tolerant of predators and more supportive of lethal control in dealing with them. The index value represents the proportion of mutualists in a given area, or the number of people exhibiting mutualist scores divided by the total number of people. Index values closer to 0 indicate a population that leans towards a domination perspective, and values closer to 1 indicate a population that leans towards mutualism. We also reviewed the wildlife action plans, regulations, and legislation as they might apply to puma conservation for the states identified as having suitable habitat.

## Results

We identified 17 areas in the Upper Midwest, Ozarks, Appalachia, and New England that met all of the minimal habitat suitability requirements, of which 13 met our stricter 10,000 km$^2$ size requirements as well (Fig. 2; Table 2). The 17 patches identified ranged in size from 6024 to 59,462 km$^2$, mean sociocultural index values from 0.31 to 0.548, percentage public land from 3 to 80%, mean human population density from 1.76 to 35.78 people/km$^2$, and mean livestock density from 1.48 to 8.83 animals/km$^2$ (Table 2).

Light and dark green show individual patches that are adjacent, but separated by unsuitable habitat, highways in most cases. These areas are likely to have some gene flow between the two, but contain sufficiently unstable habitat to be modeled as distinct areas. Note the red circle encompassing northern Vermont and New Hampshire in Fig. 2a and the close up in Fig. 2b. This is an example of our conservative methods that likely underestimate habitat where pumas could survive. Highways divided the area in the red circle into habitat patches too small to meet our threshold sizes, however traffic volumes in northern New England are likely so low as to allow connectivity across these areas. Even if pumas do not thrive in this area, but are able to move through it, the surrounding patches are likely to benefit from increased gene flow.

Most states that contained potential puma habitat patches list pumas as extirpated, and some retain laws and regulations that will impact future puma dispersal, establishment, and management (Table 3). For example, pumas are listed as endangered under the state Endangered Species Acts of New York, Vermont, South Carolina, Georgia, and Michigan; and they are protected as a species of special concern under the state Endangered Species

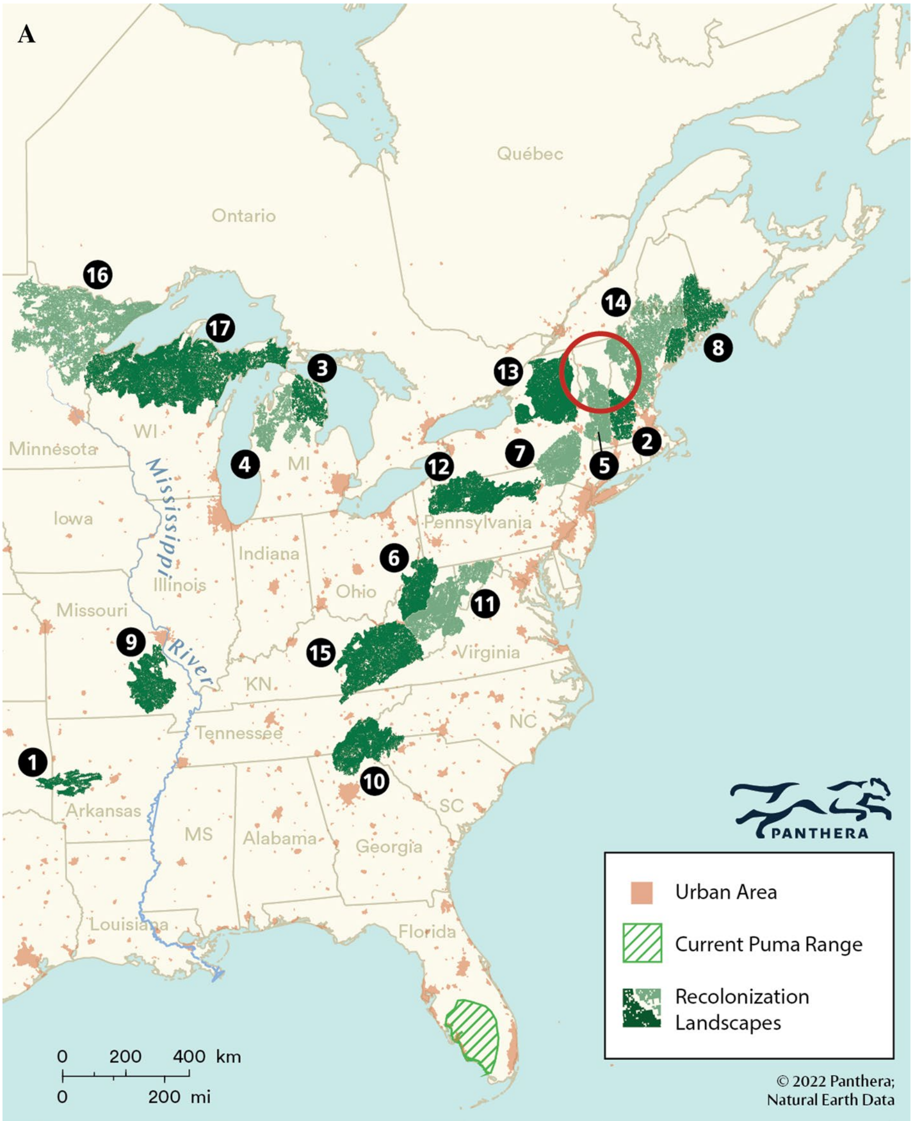


**Fig. 2** **a** Overview of Potential habitat patches that could support pumas identified by our analyses (shown in light and dark green) in the eastern United States, in relation to urban areas (shown in orange). **b** Close up of identified suitable areas for puma recolonization in the New England. (Color figure online)

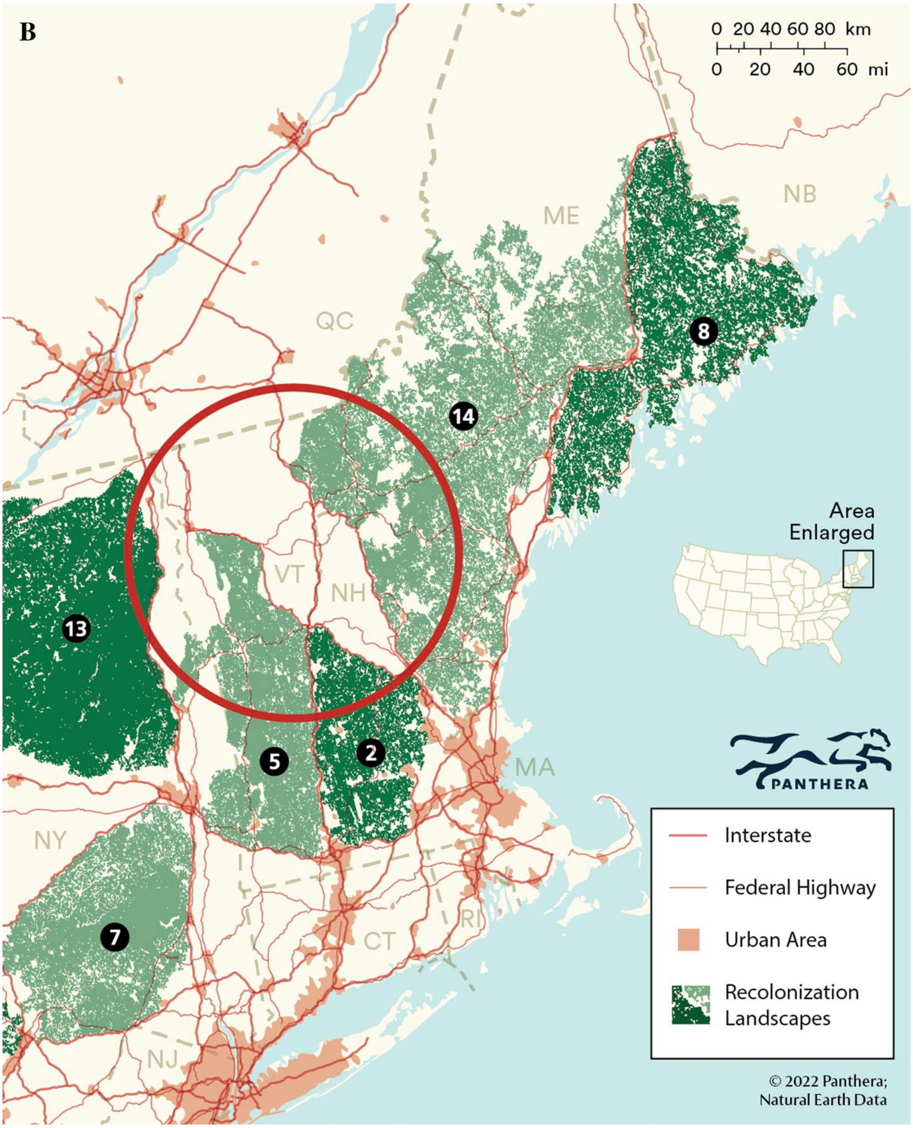


**Fig. 2** (continued)

**Table 2** Potential puma habitat patches and habitat suitability values, listed in order of increasing size

| Patch number | Area name | Patch size ($km^2$) | Percent public land | Human density (people/km2) | Socio-cultural index | Livestock density (animals/$km^2$) |
|---|---|---|---|---|---|---|
| 1 | Ouachita Mountains | 6024 | 80 | 1.76 | 0.31 | 8.83 |
| 2 | Green Mountains East | 6517 | 14 | 35.78 | 0.522 | 3.28 |
| 3 | Michigan East | 7773 | 45 | 4.76 | 0.346 | 2.93 |
| 4 | Michigan West | 9639 | 46 | 9.75 | 0.383 | 4.01 |
| 5 | Green Mountains West | 11.874 | 22 | 13.69 | 0.548 | 5.55 |
| 6 | Allegheny Plateau | 12.040 | 3 | 11.55 | 0.35 | 7.34 |
| 7 | Catskill Mountains | 12.451 | 15 | 18.34 | 0.427 | 4.77 |
| 8 | Maine East | 12.831 | 5 | 8.87 | 0.445 | 1.48 |
| 9 | Ozark Plateau | 14.341 | 34 | 8.11 | 0.317 | 8.05 |
| 10 | Great Smoky South | 17.099 | 53 | 19.23 | 0.394 | 4.23 |
| 11 | Appalachian North | 21.204 | 29 | 9.1 | 0.353 | 6.39 |
| 12 | Allegheny North | 21.582 | 42 | 7.75 | 0.367 | 4.96 |
| 13 | Adirondack Mountains | 25.162 | 42 | 5.74 | 0.397 | 3.78 |
| 14 | Maine West | 25.857 | 13 | 14.55 | 0.423 | 1.88 |
| 15 | Appalachian South | 29.481 | 9 | 17.43 | 0.351 | 3.38 |
| 16 | Minnesota North Woods | 39.831 | 54 | 2.66 | 0.42 | 1.69 |
| 17 | Wisconsin-UP | 59.462 | 43 | 2.95 | 0.38 | 2.55 |

Each patch identified meets the minimum thresholds for areas that could support a sufficiently large puma population to avoid genetic drift and inbreeding depression

Act in Minnesota. When prioritizing potential puma recovery areas, previously established legal protections could be regarded as an invisible component of habitat suitability.

## Discussion

Pumas are currently dispersing into the Midwest (LaRue et al. 2012), and eventually we expect there to be breeding populations in the East, though it may take considerable time. For example, it took nearly 20 years for pumas to expand beyond the Black Hills in South Dakota across 100 miles of human-dominated landscapes to establish a new breeding population in the Pine Ridge area of Nebraska (LaRue and Nielsen 2016). Patches closer to source populations in the West could be recolonized sooner than those farther away, and could serve as important sources for pumas to continue eastward recolonization.

**Table 3** A review of puma status under state endangered species law and wildlife action plans in states that overlap viable habitat patches

| State | Primary wildlife authorities: agency & board | Legal status, current governing laws, & policy overview | Patch number |
|---|---|---|---|
| Arkansas | Agency: Arkansas Game and Fish Commission<br>Board: Arkansas Game and Fish Commission | State-level endangered, threatened, or special concern species designations do not exist, and thus pumas cannot be listed as such. Not identified as a Species of Greatest Conservation Need (SGCN) in the 2015 Wildlife Action Plan (Fowler 2015) | 1 |
| Georgia | Agency: Wildlife Resources Division, Georgia Department of Natural Resources<br>Board: Georgia Board of Natural Resources | Florida panther (*Puma concolor coryi*) listed as endangered under state endangered species law (https://law.justia.com/codes/georgia/2020/). Also a High Priority–GA's preferred terminology for a SGCN–species in the 2015 Wildlife Action Plan (Georgia Department of Natural Resources, Wildlife Resources Division 2015). State law identifies pumas (*Puma concolor*) as a game species (https://regulations.justia.com/states/georgia/) but prohibits any hunting season (https://regulations.justia.com/states/georgia/) | 10 |
| Kentucky | Agency: Kentucky Department of Fish & Wildlife Resources, Kentucky Tourism, Arts and Heritage Cabinet<br>Board: Kentucky Fish and Wildlife Commission | Not listed under state endangered species law (Kentucky Department of Fish & Wildlife Resources 2022), not identified as a SGCN in the 2015 Wildlife Action Plan (Kentucky Department of Fish and Wildlife Resources 2013) | 15 |
| Maine | Agency: Maine Department of Inland Fisheries & Wildlife | Not listed under state endangered species law (Maine Department of Inland Fisheries and Wildlife 2015a, b), not identified as a SGCN in the 2015 Wildlife Action Plan (Maine Department of Inland Fisheries and Wildlife 2015a, b) | 8, 14 |
| Massachusetts | Agency: Division of Fisheries & Wildlife, Massachusetts Department of Fish and Game<br>Board: Massachusetts Fisheries and Wildlife Board | Not listed under state endangered species law (https://regulations.justia.com/states/massachusetts/), not identified as a SGCN in the 2015 Wildlife Action Plan (Massachusetts Division of Fisheries and Wildlife 2015) | 2, 5 |
| Michigan | Agency: Michigan Department of Natural Resources<br>Board: Michigan Natural Resources Commission | Puma (*Puma concolor*) listed as endangered under state endangered species law (https://regulations.justia.com/states/michigan/), not identified as a SGCN in the 2015 Wildlife Action Plan (Michigan Department of Natural Resources 2015) | 3, 4 |

**Table 3** (continued)

| State | Primary wildlife authorities: agency & board | Legal status, current governing laws, & policy overview | Patch number |
|---|---|---|---|
| Minnesota | Agency: Minnesota Fish and Wildlife Division, Department of Natural Resources | Puma (*Puma concolor*) listed as a species of special concern under state endangered species law (https://regulations.justia.com/states/minnesota/.), but that status does not confer the protection of endangered or threatened species(https://law.justia.com/codes/minnesota/2021/.) However, it does automatically make it a SGCN in the 2015 Wildlife Action Plan(Minnesota Department of Natural Resources 2015) No open season for pumas(https://law.justia.com/codes/minnesota/2021/), and not on the list of animals that may be killed if causing damage(https://law.justia.com/codes/minnesota/2021/) | 16 |
| Missouri | Agency: Missouri Department of Conservation<br>Board: Missouri Conservation Commission | Not listed under state endangered species law(Missouri Department of Conservation 2021), not identified as a SGCN in the 2015 Wildlife Action Plan(Missouri Department of Conservation (2015) | 9 |
| New Hampshire | Agency: New Hampshire Fish and Game Department<br>Board: New Hampshire Fish and Game Commission | Not listed under state endangered species law(https://regulations.justia.com/states/new-hampshire/), not identified as a SGCN in the 2015 Wildlife Action Plan(https://www.wildlife.state.nh.us/wildlife/wap.html). Taking or killing mountain lions is prohibited, except in cases of self or property protection(https://law.justia.com/codes/new-hampshire/2021/); however, the director of Fish & Game may take measures they deem necessary for controlling this species should they "become a nuisance in any part of the state." (https://law.justia.com/codes/new-hampshire/2021/) | 2 |
| New York | Agency: New York Department of Environmental Conservation | Puma (*Puma concolor*) listed as endangered under state endangered species law(https://regulations.justia.com/states/new-york/New York Current and Proposed Status of All Species on Proposed List.), but in-process changes first drafted in 2019 propose removal(https://www.dec.ny.gov/docs/wildlife_pdf/masterlistpropreg.pdf) Not identified as a SGCN in the 2015 Wildlife Action Plan(https://www.dec.ny.gov/docs/wildlife_pdf/swapfinaldraft2015.pdf) | 5, 7, 12, 13 |

**Table 3** (continued)

| State | Primary wildlife authorities: agency & board | Legal status, current governing laws, & policy overview | Patch number |
|---|---|---|---|
| North Carolina | Agency: North Carolina Wildlife Resources Commission<br>Board: North Carolina Wildlife Resources Commission | Although the Eastern Mountain Lion (*Puma concolor couguar*) was removed from the federal endangered species list in 2018, as of an October 1st, 2021 update to North Carolina's endangered species list, *Puma concolor* was still identified as federally endangered in North Carolina(North Carolina Administrative Code (2021)<br>Not identified as a SGCN in the 2015 Wildlife Action Plan(North Carolina Wildlife Resources Commission (2015) | 10 |
| Pennsylvania | Agency: Pennsylvania Game Commission<br>Board: Pennsylvania Board of Game Commissioners | Not listed under state endangered species law(https://regulations.justia.com/states/pennsylvania/), not identified as a SGCN in the 2015 Wildlife Action Plan.(Pennsylvania Game Commission (2015) | 7, 12 |
| South Carolina | Agency: Wildlife and Freshwater Fisheries Division, South Carolina Department of Natural Resources<br>Board: South Carolina Department of Natural Resources Board | Eastern Mountain Lion (*Puma concolor cougar*) listed as endangered under state endangered species law(South Carolina Code of Regulations (2022). Not identified as a SGCN in the 2015 Wildlife Action Plan (South Carolina Department of Natural Resources 2015) | 10 |
| Tennessee | Agency: Tennessee Wildlife Resources Agency<br>Board: Tennessee Fish & Wildlife Commission | Not listed under state endangered species law (Tennessee Comp Rules and Regs (2022), not identified as a SGCN in the 2015 Wildlife Action Plan (Tennessee Wildlife Resources Agency (2015) | 10, 15 |
| Vermont | Agency: Department of Fish & Wildlife, Agency of Natural Resources<br>Board: Vermont Fish & Wildlife Board | Eastern Mountain Lion (*Puma concolor couguar*) listed as endangered under state endangered species law(https://regulations.justia.com/states/vermont/), and is identified as a SGCN of medium (as opposed to high) priority in the 2015 Wildlife Action Plan(Vermont Fish and Wildlife Department 2015) | 5 |
| West Virginia | Agency: Wildlife Resources Section, Division of Natural Resources, West Virginia Department of Commerce | State-level endangered, threatened, or special concern species designations do not exist, and thus pumas cannot be listed as such. Not identified as a SGCN in the 2015 Wildlife Action Plan (West Virginia Division of Natural Resources 2015) | 6, 11, 15 |

**Table 3** (continued)

| State | Primary wildlife authorities: agency & board | Legal status, current governing laws, & policy overview | Patch number |
|---|---|---|---|
| Wisconsin | Agency: Fish, Wildlife & Parks Division, Wisconsin Department of Natural Resources<br>Board: Wisconsin Natural Resources Board | Not listed under state endangered species law(https://regulations.justia.com/states/wisconsin/), not identified as a SGCN in the 2015 Wildlife Action Plan(Wisconsin Department of Natural Resources (2015). Pumas are a protected wild animal, which means essentially any taking, attempted taking, transport, or possession of them alive or dead must be explicitly authorized by the Department of Natural Resources(https://regulations.justia.com/states/wisconsin/) | 17 |

Additional puma-related laws and regulations were also identified; this list is not exhaustive but includes those most directly related to puma protection in these states. Note, the state wildlife board is only included if the board has any degree of regulatory authority

For habitat to be considered suitable for pumas, there needs to be appropriate vegetation communities with low human use, livestock use, and highway density. Our analyses highlighted numerous large habitat patches that could support sustainable puma populations in the East. Of course, as the human footprint continues to expand, the suitable habitat we identified may shrink, reducing the number of places where puma populations can maintain genetic health without conservation interventions. For example, our analyses did not identify southern Florida as suitable habitat to accommodate sustainable puma populations, even though it currently hosts the only breeding population of pumas in the East. However, a recent analysis has revealed that this population will require further conservation support via the translocation of pumas from elsewhere to boost the genetic diversity among Florida pumas (locally referred to as panthers) to maintain a viable puma population into the future (van de Kerk et al. 2019).

Interstates played a large role in separating potential puma habitat patches in our results, especially in the New England states (Fig. 2a and b): Vermont, New Hampshire, Massachusetts, and Maine. There are a few instances in which adjacent areas would be considered one large patch if they were not separated by interstates (e.g., Michigan West and Michigan East; Allegheny Plateau, Appalachian North, and Appalachian South; Fig. 2). Dispersing pumas, which carry vital genetic material between habitat patches and puma populations and help restore genetic health, will attempt to cross major highways and may even be successful sometimes (e.g., Hawley et al. 2016). Therefore, many of the divisions between patches in our results may in fact be somewhat permeable from a gene flow perspective, and what appears as several smaller patches could be connected to create fewer, larger patches. Our analyses treated interstates as uniform across their length, but a better metric to determine what sections of specific interstates are and are not permeable to pumas would be traffic volume. For example, Interstate 93, which runs north–south in New Hampshire, has very low traffic volume in the north and higher use in the south, so we would expect the southern portion to be less permeable to pumas than the northern portion. Unfortunately, we currently lack specific threshold information about what traffic loads restrict pumas and impact their metapopulation dynamics (e.g., Gustafson et al. 2019).

We did not rank patches in terms of potential suitability for pumas, because they all met the conservation thresholds we set and therefore all could host puma populations in the future. Nevertheless, the metrics we used to delineate these areas, and those we summarize in Table 2, may be useful for conservation planning comparison. For example, the larger the size of an area of suitable habitat, generally the greater chance that a resident flora or fauna population will remain viable (Bender et al. 1998). The lowest human and livestock densities might be useful in identifying areas where pumas are least likely to experience conflict with human communities, and the highest sociocultural index values (Manfredo et al. 2021) may be indicative of potential tolerance and the willingness of local people to coexist with large carnivores.

Pumas play an important role in regulating prey, producing carrion for scavengers, and providing ecosystem services, each of which contributes to ecological resilience and healthy human communities (Barry et al. 2019; LaBarge et al. 2022). Pumas may more directly benefit humans by reducing automobile collisions with deer, protecting human lives and reducing expensive damages (Gilbert et al. 2021). However, these and other environmental benefits are unlikely to convince all members of the public to support puma recovery. Education and outreach will play an essential role in communicating the potential costs and benefits of living sympatrically with large carnivores as they recolonize their historic range (López-Bao et al. 2017; Gilbert et al. 2021).

Pumas pose real and perceived risks to domestic animals and humans, and so our results also serve as a map to identify priority areas for investing in outreach, education, and policy instruments before pumas reestablish in the East (Madden 2004; Baruch-Mordo et al. 2011; Redpath et al. 2013). While some details of human-puma conflict may be unpredictable in areas newly colonized by pumas, important patterns of conflict are readily inferred from those documented following other carnivore restoration or recolonization, such as gray wolves (*Canis lupus*) in North America and Europe. For example, there is lively research debate and public discord surrounding the relationship between wolf recovery and hunter opportunity (Garrot et al. 2005; Vucetich et al. 2005; Brodie et al. 2013; MacNulty et al. 2016; Wikenros et al. 2020). Livestock-carnivore conflict and how to manage reestablished carnivore populations on rangelands are similarly contentious topics (e.g., lethally removing wolves to protect livestock; Bradley et al. 2015; Santiago-Avila et al. 2018).

Anticipating conflict and finding ways to get ahead of issues common to other carnivore recovery efforts could help facilitate puma recovery. Framing this in the context of wolf restoration, public acceptance of wolves decreased among some stakeholders following their return (Ericsson and Heberlein 2003; Treves et al. 2013), even as broader public attitudes (e.g., US, Sweden) became more positive (George et al. 2016; Heberlein and Ericsson 2008). Although some have suggested that decreased acceptance of wolves within an area tends to accompany their occurrence (e.g., Karlsson and Sjöström, 2007), recent analyses in the U.S. show this effect depends upon the stakeholder groups with which one identifies (Carlson et al. 2020). Specifically, a large-scale survey of Americans residing within and outside wolf recovery areas found ranchers who lived within those areas were more negative towards wolves than ranchers who lived outside of those areas; conversely, environmentalists living within wolf recovery areas were actually more positive towards wolves than environmentalists living outside these areas. While it may be tempting to assume similar social conflict would follow puma restoration, differences in the behavior and ecology of pumas and wolves (e.g., ambush vs. coursing predation; cryptic vs. visible behavior, etc.) may lead to pumas being perceived as less threatening to livestock and game populations. Likewise, regional differences in values (see Manfredo et al. 2020) and political ideologies change the cultural context in which conflicts with carnivores are perceived. Thus, we caution readers against assuming the type of conflict that has accompanied wolf restoration efforts will also accompany puma restoration.

Our analyses suggest that ample habitat exists in the eastern US to support pumas, and ongoing records of puma dispersal in the Midwest show that individuals are on their way. Future analyses could help predict how long it might take to see breeding pumas establish in the east. The question remains, however, whether the people of the East are willing to coexist with pumas when they arrive. We suggest proactive efforts (as opposed to reactive, post-problem management) to help residents avoid negative impacts of pumas, will be the most useful for promoting coexistence.

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**Data availability** Each of the datasets analyzed in this study are available from the sources described in Table 1.

## Declarations

**Competing interest** The authors have no competing interests as defined by Springer, or other interests that might be perceived to influence the results and/or discussion reported in this paper.

**Ethical approval** No institutional approval or ethical review was needed in order to conduct this study.

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