March 4, 2024

Public Comments Processing
Attn: FWS–HQ–NWRS–2022–0106
U.S. Fish and Wildlife Service
5275 Leesburg Pike
MS: PRB (JAO/3W)
Falls Church, VA 22041–3803

RE: Comments on proposed regulations for National Wildlife Refuge System regarding Biological Integrity, Diversity, and Environmental Health ("BIDEH") and Updated BIDEH Policy, 89 Fed. Reg. 7345 (Feb. 2, 2024)

Submitted via regulations.gov, Docket No. FWS–HQ–NWRS–2022–0106

Dear Assistant Secretary for Fish and Wildlife and Parks Estenoz,

Sierra Club writes to identify concerns with the proposed regulations addressing the requirement to maintain, restore, and enhance the biological integrity, diversity, and environmental health ("BIDEH") of the National Wildlife Refuge System (Refuge System), as required by the National Wildlife Refuge System Improvement Act of 1997, and the accompanying proposed updates to the BIDEH policy.[1] Sierra Club strongly supports the Fish and Wildlife Service's recognition of the need to ban predator control of native predators on Refuge System lands, and to provide direction for requiring mitigation of greenhouse gas emissions, but urges the Service to strengthen the proposed regulations as detailed below, to better ensure fulfillment of the BIDEH mandate.

The Sierra Club was founded in 1892 and is the nation's oldest grassroots environmental organization. The Sierra Club is incorporated in California, and has approximately 690,490 members nationwide. The organization is dedicated to the protection and preservation of the environment. The Sierra Club's mission is to explore, enjoy and protect the wild places of the

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[1] *See* 89 Fed. Reg. 7345 (Feb. 2, 2024).

earth; to practice and promote the responsible use of the earth's ecosystems and resources; and to educate and enlist humanity to protect and restore the quality of the natural and human environments. One of the Sierra Club's main national initiatives, the Conservation and Outdoors Campaign, tackles pressing environmental problems including the extinction and climate change crises, and threats to wildlife. Sierra Club has long advocated for protections for wildlife, and for proper management of National Wildlife Refuge system lands as required under the National Wildlife Refuge System Administration Act of 1966 as amended by the National Wildlife Refuge System Improvement Act of 1997, 16 U.S.C. § 668dd–668ee, and other applicable laws.

As the Service recognizes, Congress specified that "[t]he mission of the System is to administer a national network of lands and waters for the conservation, management, and where appropriate, restoration of the fish, wildlife, and plant resources and their habitats within the United States for the benefit of present and future generations of Americans."[2] Further, "in administering the System" the Secretary of Interior "shall…provide for the conservation of fish, wildlife, and plants and their habitats within the System" and "ensure that the biological integrity, diversity, and environmental health of the System are maintained for the benefit of present and future generations of Americans."[3]

To effectuate these requirements, Sierra Club urges the Service to address the concerns identified and explained below.

1. The Proposed Regulations Should Be Revised to Avoid Introducing Ambiguity Regarding Restoration and Enhancement

The proposed regulations state: "We will maintain and, where **necessary and appropriate**, restore and enhance the biological integrity, diversity, and environmental health of national wildlife refuges, both individually and as a network of intact, functioning, and resilient habitats for fish, wildlife, and plants, for the benefit of present and future generations of Americans."[4] In contrast, the Refuge Administration Act states: "The mission of the System is to administer a national network of lands and waters for the conservation, management, and **where appropriate**, restoration of the fish, wildlife, and plant resources and their habitats within

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[2] 16 U.S.C. § 668dd(a)(2).

[3] *Id*. at § 668dd(a)(4)(A)-(B).

[4] Proposed 50 C.F.R § 29.3 (emphasis added). 89 Fed. Reg. 7350.

the United States for the benefit of present and future generations of Americans."[5] The Service should not unnecessarily narrow the circumstances under which restoration and enhancement will occur by introducing a term that the statute does not require, and thereby potentially imposing a requirement to find that restoration and enhancement is "necessary" when the statute conceived that restoration and enhancement would occur when deemed appropriate, and not necessarily only when "necessary."

2. The Service Should Further Clarify the Proposed Definition of Connectivity

The proposed regulations define "connectivity" to mean "the degree to which landscapes, waterscapes, and seascapes allow species to move freely and ecological processes to function unimpeded."[6] The Service should clarify that the concept of connectivity includes habitats that support maintaining populations with the genetic and demographic connectivity necessary for long-term persistence of populations. As written, the definition potentially could be misunderstood as applying only to habitat required for movement or migration, rather than also including habitat that supports resident populations ("corridor dwellers") that bridge other populations, which can be critically important for "low-mobility" species.[7]

3. The Service Should Clarify the Provisions Related to Climate Change Mitigation

The Service properly recognizes that Refuge managers have an obligation to require greenhouse gas (GHG) emissions reductions as mitigation to ensure that management actions contribute to and do not detract from maintaining biological integrity, diversity, and

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[5] 16 U.S.C.§ 668dd(a)(2) (emphasis added).

[6] Proposed 50 C.F.R § 29.3(b). 89 Fed. Reg. 7351.

[7] *See, e.g*., Averill-Murray RC, Darst CR, Strout N, Wong M. 2013. Conserving population linkages for the Mojave Desert Tortoise (*Gopherus agassizii*). *Herpetological Conservation and Biology* 8(1):1–15 at 2 ("Low-mobility species like the Mojave Desert Tortoise require corridors that contain habitat attributes within the matrix for sustaining individuals for extended periods or even multi-generational populations ("corridor dwellers"), in contrast to species that may pass through corridors between protected areas in days or weeks, especially at large spatial scales (Beier and Loe 1992)."); Barrows CW, Fleming KD, Allen MF, 2011. Identifying Habitat Linkages to Maintain Connectivity for Corridor Dwellers in a Fragmented Landscape. *The Journal of Wildlife Management* 75(3):682–691.

environmental health.[8] To better effectuate that obligation, the Service should both clarify the definition of climate change mitigation and provide better direction to ensure that Refuge managers require such mitigation.

The proposed regulations define "climate change mitigation" to mean "measures taken to reduce the amount and speed of future climate change by reducing emissions of heat-trapping gases or removing carbon dioxide from the atmosphere, including by improving ecosystem capacity for biological carbon sequestration."[9] The Service should specify that such "mitigation" must result in net emissions reductions via increased removal on a time-scale that reflects the need for urgent near-term emissions reductions. For example, decision-makers may sometimes irrationally assert that logging activities will have emissions benefits by replacing older, larger trees with sequestration rates per mass that have plateaued with new young trees that have higher sequestration rates per mass, ignoring, among other factors, that the lost carbon storage from the older larger trees, and the greater total sequestration of the older trees due to their large mass results in a net flux of CO_2 to the atmosphere due to such logging (rather than increased carbon removal) *during the near term time periods when it is most urgent to achieve drastic reductions*.[10] The Service should amend the proposed definition to ensure that Refuge managers

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[8] *See* proposed 50 C.F.R § 29.3(c)(1). 89 Fed. Reg. 7351.

[9] Proposed 50 C.F.R § 29.3(b). 89 Fed. Reg. 7351.

[10] *See, e.g.*, Rogers BM, Mackey B, Shestakova TA, Keith H, Young V, Kormos CF, DellaSala DA, Dean J, Birdsey R, Bush G, Houghton RA and Moomaw WR (2022) Using ecosystem integrity to maximize climate mitigation and minimize risk in international forest policy. *Front. For. Glob. Change* 5:929281. doi: 10.3389/ffgc.2022.929281 at 6-7 (discussing carbon justifications for converting mature primary forests into secondary forests and concluding that "From a carbon balance perspective, converting primary forests into young forests logged for biomass energy, wood supply, or other uses does not offset the original conversion emissions for many decades to centuries … creating a large carbon debt on policy-relevant timescales (generally years to 1–3 decades). Hence the size, longevity, and stability of accumulated forest carbon stocks, including in the soils, are important mitigation metrics in addition to the rate of annual sequestration.") (internal citations omitted); *see also* Law et al. (2022) Creating Strategic Reserves to Protect Forest Carbon and Reduce Biodiversity Losses in the United States, *Land*, 11, 721, https://doi.org/10.3390/land11050721 at 4-5 of 15 (discussing loss of carbon storage from converting mature forests into young forests even when storage in wood products is considered, and how unharvested mature forest stores more carbon compared to harvested even after 120 years from harvest); *id*. at 6 of 15 (explaining that "*eventual carbon neutrality* does not mean *climate neutrality"* because the timing of achieving net carbon removal determines whether impacts to humans and wildlife from sea ice loss and sea-level rise and climate disasters will occur or be avoided).

rationally consider whether actions intended to reduce emissions by increasing carbon removal will achieve net emissions reductions on a time-scale and in a manner that is actually consistent with addressing the climate emergency.

Furthermore, the regulations should clarify that employing adaptation strategies does not eliminate the need for climate change mitigation. To address the emergency need for emissions reductions, Refuge managers should require climate change mitigation for activities that would otherwise contribute to climate change, regardless of whether adaptation strategies are also in place or required. In light of the threat that climate change poses to many species and habitats across the Refuge System, ensuring that refuge management "contributes to and does not diminish the biological integrity, diversity, and environmental health of refuges and the Refuge System"[11] plainly necessitates mitigation to reduce emissions that would contribute to climate change.

4. The Service Should Clarify the Provisions Related to Restricting Predator Control to Narrow or Eliminate Exemptions from the Restrictions

The proposed regulations prohibit native "predator control" except for under certain limited circumstances, but state that a number of "actions" are not considered by the Service to be predator control.[12] Those actions include: "Use of barriers or nonlethal deterrents to protect the public, property, or vulnerable species, but **that are not intended to** reduce native predator populations."[13] Instead of basing this definition on the *intent*, the Service should instead consider whether the barrier or nonlethal deterrents in question *have the effect of* reducing native predator populations. Regardless of intent, the Service should treat such barriers as predator control if they have the effect of reducing native predator populations, and therefore should allow them only under the narrow circumstances prescribed in proposed 50 C.F.R. § 29.3(d)(1).

The proposed definition of "predator control" excludes "actions necessary to protect public health and safety and those enumerated under paragraph (d)(1) of this section."[14] Proposed paragraph (d)(1)(i) in turn provides that "Agency removal of native predator(s) solely

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[11] Proposed 50 C.F.R § 29.3(a). 89 Fed. Reg. 7350.

[12] Proposed 50 C.F.R § 29.3(d)(1)(i)-(iv). 89 Fed. Reg. 7351–52.

[13] Proposed 50 C.F.R. § 29.3(d)(1)(ii)). 89 Fed. Reg. 7,352 (emphasis added).

[14] Proposed 50 C.F.R § 29.3(b). 89 Fed. Reg. 7351.

to protect public health and safety" is not "predator control."[15] To avoid the potential for confusion and misinterpretation resulting from this redundancy, the definition of "predator control" should instead state that "predator control" excludes only "actions enumerated under paragraph (d)(1) of this section." Furthermore, paragraph (d)(1)(i) should read: "Agency removal of native predator(s) solely as necessary to protect public health and safety from an imminent threat."

The proposed regulations also state: "Compatible, refuge-approved recreational hunting and fishing opportunities that do not compromise maintaining biological integrity, diversity, and environmental health **on the refuge**" are not "predator control."[16] First, the Service should not exclude "recreational hunting" from the definition of predator control where recreational hunts for the species in question are part of an overall program aimed either at reducing predator populations or at bolstering/increasing prey populations by controlling predators. Second, the Service should not exclude recreational hunting from the definition of predator control where programs for predator control for the species in question are in place outside the Refuge. In other words, for species that are already subject to efforts to reduce their populations outside Refuge lands, the Service should not exclude hunts on Refuge lands from the definition of "predator control" and should allow such hunts only where consistent with the requirements in proposed 50 C.F.R. § 29.3(d)(1).

The regulations should also specify that the definition of "predator control" encompasses lethal and nonlethal removal of predators for the purpose of protecting livestock, such as cattle, sheep, or other domesticated animals.[17]

Finally, the regulations should more broadly restrict the hunting and trapping of native carnivores due to the negative ecological consequences of many hunting and trapping practices (such as baiting, hounding, aerial gunning, and the use of traps and snares) on native carnivores and on non-target species.[18]

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[15] Proposed 50 C.F.R § 29.3(d)(1)(i). 89 Fed. Reg. 7351–52.

[16] Proposed 50 C.F.R. § 29.3(d)(1)(iv)). 89 Fed. Reg. 7352 (emphasis added).

[17] Additional detail regarding this point is provided in a separate comment letter, signed onto by the Sierra Club and over 140 other non-governmental organization signatories. Sierra Club incorporates those comments by reference here.

[18] Additional details supporting this point are provided in a separate comment letter, signed onto by the Sierra Club and over 140 other non-governmental organization signatories. Sierra Club incorporates those comments by reference here.

5. The Service Should Prohibit Use of Pesticides with Adverse Impacts on Individuals from Non-target Species

Proposed 50 C.F.R. § 29.3(d)(5) states: "We may allow the use of pesticides, following review and approval of their use as part of an integrated pest management plan, when necessary to meet statutory requirements, fulfill refuge purposes, and ensure biological integrity, diversity, and environmental health. **Such use must not result in adverse effects on populations of nontarget species**."[19] The Service should clarify that pesticide use may be prohibited even where there is not a population-level adverse impact on the nontarget species (i.e., that pesticide use may be prohibited based on adverse impacts to individual members of a species).

If you have any questions about these comments, please contact me at (202) 548-4584 or karimah.schoenhut@sierraclub.org.

Sincerely,

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[19] 89 Fed. Reg. 7352 (emphasis added).

CITED MATERIALS

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CONSERVING POPULATION LINKAGES FOR THE MOJAVE DESERT TORTOISE (*GOPHERUS AGASSIZII*)

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***Abstract.*—Conservation of Mojave Desert Tortoises is founded on a set of tortoise conservation areas (TCAs) established across the range of the species. Limitations of the existing reserve design and increasing development pressures on the intervening habitat matrix underscore the need to conserve linkages between existing TCAs. We modeled linkages between TCAs using least-cost corridors based on an underlying model of suitable tortoise habitat. Results indicate that TCAs contain 55% of total historic habitat (45,340 km^2). A minimum linkage network would contain 16,282 km^2 of habitat (20% historic). This combined area of 61,622 km^2 represents an initial framework to develop a conservation network for the species, taking into account large areas of existing high-intensity human uses such as military operations and off-highway-vehicle recreation. Models that assume more permeable habitat to tortoise connectivity reveal much broader linkages, but approximately 700 km^2 of habitat within the minimum linkages are already at risk of permanent habitat loss through solar energy development. Additional conservation of occupied habitat adjacent to the minimum linkages and existing TCAs would provide security against edge effects and population declines within conservation areas, especially given limitations in existing reserve architecture. Application of these linkage models will require refinement at the local level, and questions remain about the ultimate ability of a conservation network based on these models to support viable tortoise populations and accommodate climate change. Nevertheless, conservation decisions cannot be delayed while awaiting final answers to all relevant questions. In areas proposed for permanent habitat conversion, critical linkages may be severed before they are protected.**

Key Words.—connectivity; conservation; habitat fragmentation; least-cost corridor

INTRODUCTION

Habitat loss and fragmentation are prevalent threats to biodiversity (Yiming and Wilcove 2005; Venter et al. 2006). Fragmented, isolated populations are subject to demographic, environmental, and genetic forces that can act independently or together to create a “vortex” of extinction (Wilcox and Murphy 1985; Gilpin and Soulé 1986; Fagan and Holmes 2006). Connecting protected areas with linkages is a way to increase the effective area of reserves and the population size of at-risk species (Crooks and Sanjayan 2006). In addition to the benefits of buffering small or low-density populations in protected areas, preservation of natural levels of connectivity between these areas may be critical to facilitate gene flow and to prevent habitat specialization and genetic divergence between otherwise isolated populations (Frankham 2006). Preserving connectivity also may allow species to adapt to or allow for natural range shifts in response to changing environmental conditions (Meffe and Carroll 1994; Krosby et al. 2010). Therefore, protected areas by themselves may not provide adequate long-term protection to biodiversity without considering the context of the reserve, its shape, and the “matrix” of the surroundings, which may contain a variety of habitats of different quality (Ricketts 2001; Prugh et al. 2008; Prevedello and Vieira 2010). A well-connected network of reserves increases chances of maintaining viable populations of a particular species over a single reserve or isolated reserves (e.g., Carroll et al. 2003).

The Mojave Desert Tortoise (*Gopherus agassizii*) was listed as threatened under the U.S. Endangered Species Act in 1990 due to reports of population declines across the species’ distribution (see Berry and Medica [1995] for evidence of declines within local populations, but see also Bury and Corn [1995] for alternative interpretations of widespread declines) and numerous perceived threats across its range (U.S. Fish and Wildlife Service 1990). The historic distribution of the Mojave Desert Tortoise was relatively continuous across its range, broken only by major topographic barriers, such as Death Valley, California, and the Spring Mountains, Nevada (Germano et al. 1994; Nussear et al. 2009). The foundation of desert tortoise conservation and recovery across this landscape consists of 12 designated critical habitat units, which range in area from 221 to 4,130 km^2. Critical habitat, in addition to National Park Service lands and other conservation areas or easements managed for desert tortoises, constitutes the primary component of tortoise conservation areas (TCAs; U.S. Fish and Wildlife Service 2011). The minimum reserve size recommended to preserve viable populations was estimated as 2,590 km^2 (U.S. Fish and Wildlife Service 1994), and only four critical habitat units meet this threshold. Given that the quality of conserved habitat can be affected by factors present outside a preserve's boundary (Harrison and Bruna 1999), optimal reserve shape would be circular to minimize the perimeter and potential edge effects relative to the area. However, management practicalities resulted in all critical habitat units having complex perimeters, often with narrow extensions or projections into relatively unprotected habitat.

Population viability analyses indicate that, while focused management to improve adult tortoise survival could be effective in reversing population declines, the loss of large blocks of habitat in adjacent areas would be a major setback for population recovery (Doak et al. 1994; see also Reed et al. 2009). Similar analyses led to the recommendation that reserves should contain at least 10,000 adult tortoises to allow persistence > 350 y (U.S. Fish and Wildlife Service 1994). During the three most recent years of monitoring for which data are available, estimated abundances in only three (in 2009 and 2010) to five (in 2008) of the critical habitat units met this target (McLuckie et al. 2010; U.S. Fish and Wildlife Service, unpubl. data). However, some units share boundaries and form contiguous blocks (Fig. 1), and three such blocks in California include combined abundances of over 10,000 adult tortoises (Fremont-Kramer/Superior-Cronese, Fenner/Chemehuevi, and Pinto Mountains/Joshua Tree National Park/Chuckwalla).

Concentrated management of protected areas, especially those that fail to meet minimum area or abundance guidelines, has been recommended to increase desert tortoise populations, but managing the habitat matrix between protected areas is also important (U.S. Fish and Wildlife Service 1994, 2011). Habitat loss within the matrix has been increasing recently from anthropogenic pressures such as utility-scale renewable energy development (Lovich and Ennen 2011), and proposals exist for other habitat-destructive activities such as expansion of military training lands, high-speed rail lines, and new airport construction. Low-mobility species like the Mojave Desert Tortoise require corridors that contain habitat attributes within the matrix for sustaining individuals for extended periods or even multi-generational populations ("corridor dwellers"), in contrast to species that may pass through corridors between protected areas in days or weeks, especially at large spatial scales (Beier and Loe 1992). As a result, even though individual desert tortoises can make long-distance movements (Berry 1986; Edwards et al. 2004), we rarely expect desert tortoises in one protected area to traverse a long, narrow "green strip" (e.g., more narrow than that necessary to support an individual's annual activity) of "preserved" Mojave Desert habitat, with potentially habitat-degrading edge effects, to another protected area several kilometers distant (as opposed to tortoises moving several meters through a narrow barrier, such as through a culvert below a highway; Boarman et al. 1998). In this study, we integrated assessments of habitat potential and anthropogenic effects to model existing suitable habitat for the Mojave Desert Tortoise. We used this suitable habitat layer to model linkages between TCAs using least-cost corridor analysis.

MATERIALS AND METHODS

Data.—All data used in our analyses came from previously published sources: 1) TCAs (U.S. Fish and Wildlife Service 2011; compiled from multiple sources including the U.S. Fish and Wildlife Service, Bureau of Land Management, and Clark County, Nevada); 2) U.S.

TABLE 1. Pairs of conservation areas between which habitat linkages for the Mojave Desert Tortoise (*Gopherus agassizii*) were identified with least-cost corridor models.

1	Ord-Rodman	Joshua Tree National Park
2	Fremont-Kramer	Ord-Rodman
3	Superior-Cronese	Ord-Rodman
4	Ord-Rodman	Mojave National Preserve
5	Superior-Cronese	Ivanpah
6	Superior-Cronese	Death Valley National Park (west)
7	Pinto Mountains	Chemehuevi
8	Chuckwalla	Chemehuevi
9	Chemehuevi	Ivanpah
10	Ivanpah	Death Valley National Park (Greenwater Valley)
11	Ivanpah	Piute-El Dorado
12	Ivanpah	Desert Tortoise Conservation Center
13	Desert Tortoise Conservation Center	Desert National Wildlife Refuge
14	Desert Tortoise Conservation Center	Piute-Eldorado
15	Death Valley National Park (Greenwater Valley)	Mormon Mesa
16	Mormon Mesa	Lake Mead National Recreation Area
17	Desert National Wildlife Refuge	Lake Mead National Recreation Area
18	Beaver Dam Slope	Gold Butte-Pakoon
19	Beaver Dam Slope	Upper Virgin River

Geological Survey's (USGS) desert tortoise habitat potential model (Nussear et al. 2009); 3) The Nature Conservancy's Mojave Ecoregional Assessment (Randall et al. 2010. Mojave Desert Ecoregional Assessment. Available from http://conserveonline.org/workspaces/mojave/documents/mojave-desertecoregionaal-2010/@@view.html [Accessed 10 January 2012]); 4) The Nature Conservancy's Sonoran Desert Ecoregional Assessment (Conservation Biology Institute. 2009. A framework for effective conservation management of the Sonoran Desert in California. Available from http://static.consbio.org/media/reports/files/SonoranFramework_ January_20091.pdf [Accessed 10 January 2012]); and 5) the Multi-Resolution Land Characteristics Consortium's National Landcover Dataset: 2006 (NLCD; Fry et al. 2011).

Modeling suitable habitat.—The USGS model of historical habitat probability for the Mojave Desert Tortoise used presence data and a set of environmental variables to predict potential areas of desert tortoise habitat on a scale of 0–1 throughout its geographic range at 1 km^2 resolution. The model did not account for anthropogenic changes that have altered relatively high-potential habitat into areas with lower potential. We therefore used the NLCD developed-areas layer and The Nature Conservancy's "Highly Converted Areas" for the Mojave ecoregion (Randall et al. *op. cit.*) and "Conservation Category D" areas for the Sonoran ecoregion (Conservation Biology Institute *op. cit.*) to reclassify developed areas where tortoises cannot or are less likely to occur to a lower habitat potential, as described below. The "highly converted" and "category D" layers depict urban, suburban, and agricultural lands that have been heavily altered. The Nature Conservancy's ecoregional assessments were done as hexagon rasters of approximately 2.6 km^2, which are appropriate at scales greater than 1:250,000 (Randall et al. op. cit; Conservation Biology Institute op. cit).

To make the three primary datasets analytically comparable, we resampled all datasets to the same 100 m grid-cell resolution, as is commonly done with GIS datasets. We resampled the USGS habitat potential model from its 1 km grid-cell size to a 100 m grid cell with a nearest-neighbor approach using the Resample tool in ArcGIS (ESRI, Redlands, California, USA). The Nature Conservancy's Ecoregional Assessment dataset was available as hexagonal units approximately 2.5 km^2 in area as vector (polygon) files. To be compatible with our analysis, we rasterized the output to a 100 m grid cell. We downsampled the NLCD from 30 m using ArcGIS's Aggregate tool, setting the aggregation technique to Maximum. This setting took the maximum cell value from the source when determining the new value for the output cell.

We reclassified habitat potential values based on anthropogenic features from the datasets described above. We assigned areas within the NLCD as 0 habitat potential using a series of ArcGIS conditional (if/else "Con") statements if they were classified as high-intensity developed or medium-intensity developed. The high-intensity developed category includes highly developed areas where impervious surfaces account for 80–100% of the total cover. The medium-intensity developed category includes areas where impervious surfaces account for 50–79% of the total cover; these areas most commonly include single-family housing units. We assumed that the low-intensity developed category, which includes areas where impervious surfaces account for 20–49% percent of total cover, reduces tortoise occupancy potential below the baseline threshold for natural habitat without necessarily eliminating all use, so we assigned scores of 0.3 to these areas if the USGS habitat potential value was greater than or equal to 0.3. We reclassified areas categorized by The Nature Conservancy as "highly converted" and "category D" to 0 habitat potential; the highly converted layer depicts urban, suburban, and agricultural lands that have been heavily altered. Areas not affected by these anthropogenic features retained their underlying score from the USGS habitat model.

We also identified areas of contiguous non-zero cells less than a cumulative area of 1 km^2. We classified these areas as 0 habitat potential because they are isolated patches that are disconnected from contiguous habitat and are capable of supporting few tortoises (e.g., fewer than 14 adult tortoises on average; U.S. Fish and Wildlife Service, unpubl. data). Figure 1 depicts the resulting "Suitable Habitat" model. For discrete estimations of habitat area (i.e., to convert the probability model to presence/absence), we clipped the model to the 0.5 habitat-probability threshold based on 0.5 prevalence in the model dataset (Liu et al. 2005; Ken Nussear, pers. comm. 2009).

Least-cost corridor model simulation.—Least-cost path analysis uses a raster-based algorithm that weighs the minimal cost distance between source and target cells. We used five basic steps to finding least-cost corridor networks in our study landscape (cf. Sawyer et al. 2011): (1) Select the specific source and destination points; (2) create a spatially-explicit resistance surface that is weighted according to facilitating or hindering effects on the movement process; (3) calculate a minimum accumulated cost surface over the resistance surface from all cells in the study area for both the source and destination features (treating each feature as a source), creating two raster maps where every cell is assigned a value that represents the lowest possible accumulative cost from the feature to each cell; (4) use these two accumulative cost outputs to find the sum of

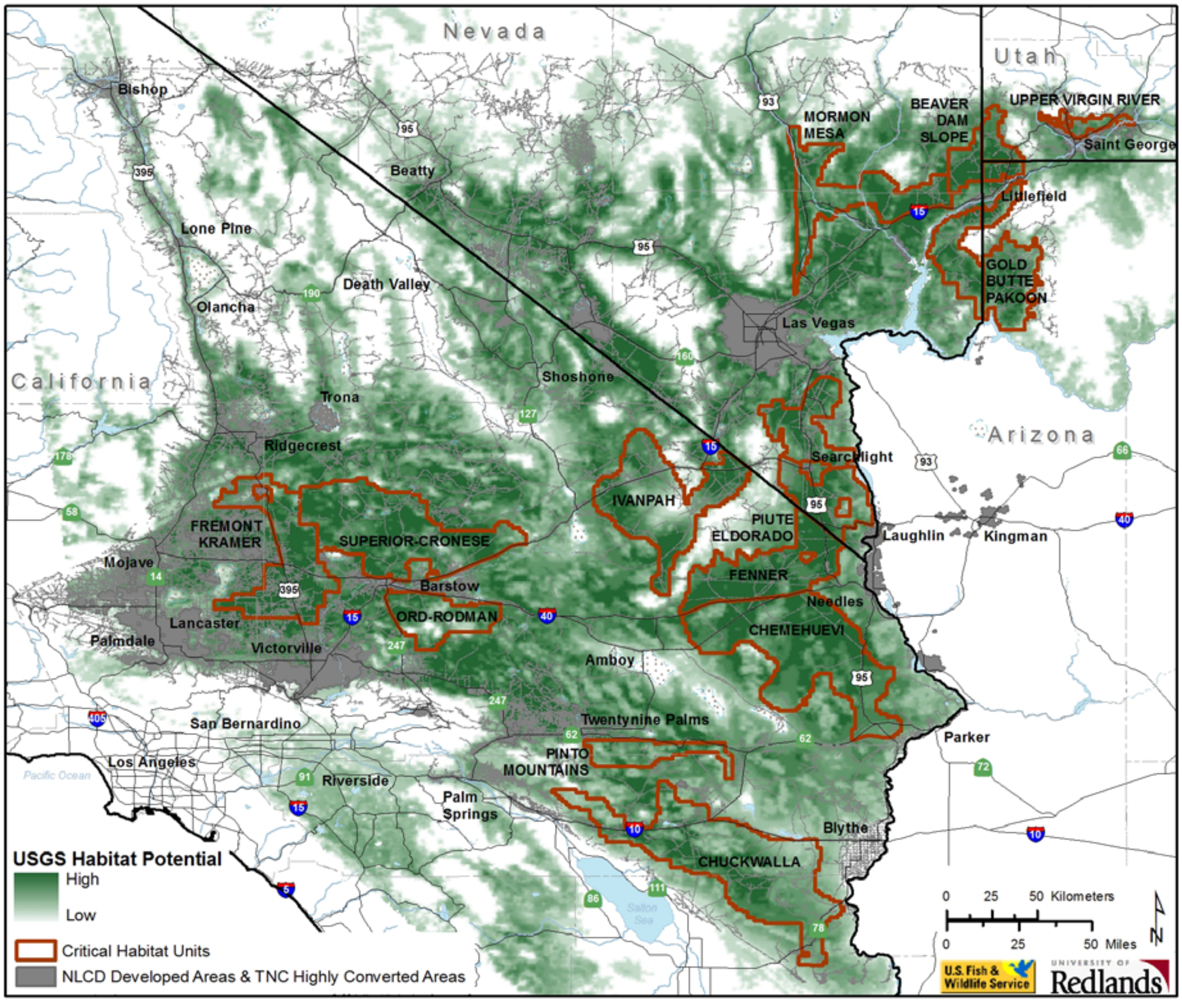

FIGURE 1. Current predicted Mojave Desert Tortoise (*Gopherus agassizii*) habitat adapted from Nussear et al. (2009).

the two surfaces at each cell. The sum of the two raster costs identifies for each cell location the least-cost path from one source to another source that passes through the cell location (ESRI. 2011. Creating a least cost corridor. ArcGIS Desktop Help 10.0. Available from http://help.arcgis.com/en/arcgisdesktop/10.0/help/index.html#//009z00000024000000.htm [Accessed 9 April 2012]); and (5) apply a maximum accumulated distance threshold to define a corridor (as opposed to a single line resulting from a least-cost path analysis).

Nineteen pairs of TCAs served as source/destination polygons for our least-cost corridor analysis (Table 1). We modeled connectivity between TCA pairs through cells of habitat capable of supporting tortoise occupancy under the premise that the Mojave Desert Tortoise is a corridor dweller. High-probability habitat corresponds to "low cost" for tortoise occupancy, so we inverted the habitat suitability surface using ESRI's Spatial Analyst arithmetic functions for use as a cost surface. Using the source polygons and the cost surface, we created a cost-distance surface for each of the source polygons defined in a pair (two surfaces per pair). These surfaces represent the accumulative cost of "traveling" over the cost surface from each cell back to the edge of the source polygon. We created these surfaces with ESRI's Spatial Analyst CostDistance function. We used ESRI's Spatial Analyst Corridor function to sum the two accumulative costs for the two input accumulative-cost rasters, thereby identifying, for each cell location, the least-cost path from the source to the destination that passes through that cell location. Because of the varying cost between each TCA pair (one pair might be geographically adjacent to one another while another pair might be separated by > 100 km), we applied a standard threshold percentage to normalize the outputs. Through an iterative process of reviewing threshold outputs, we chose a standard distance threshold of 1% for each corridor output. The associated range of cost-distance values were calculated from the total range of corridor values and applied using ESRI's Spatial Analyst Con

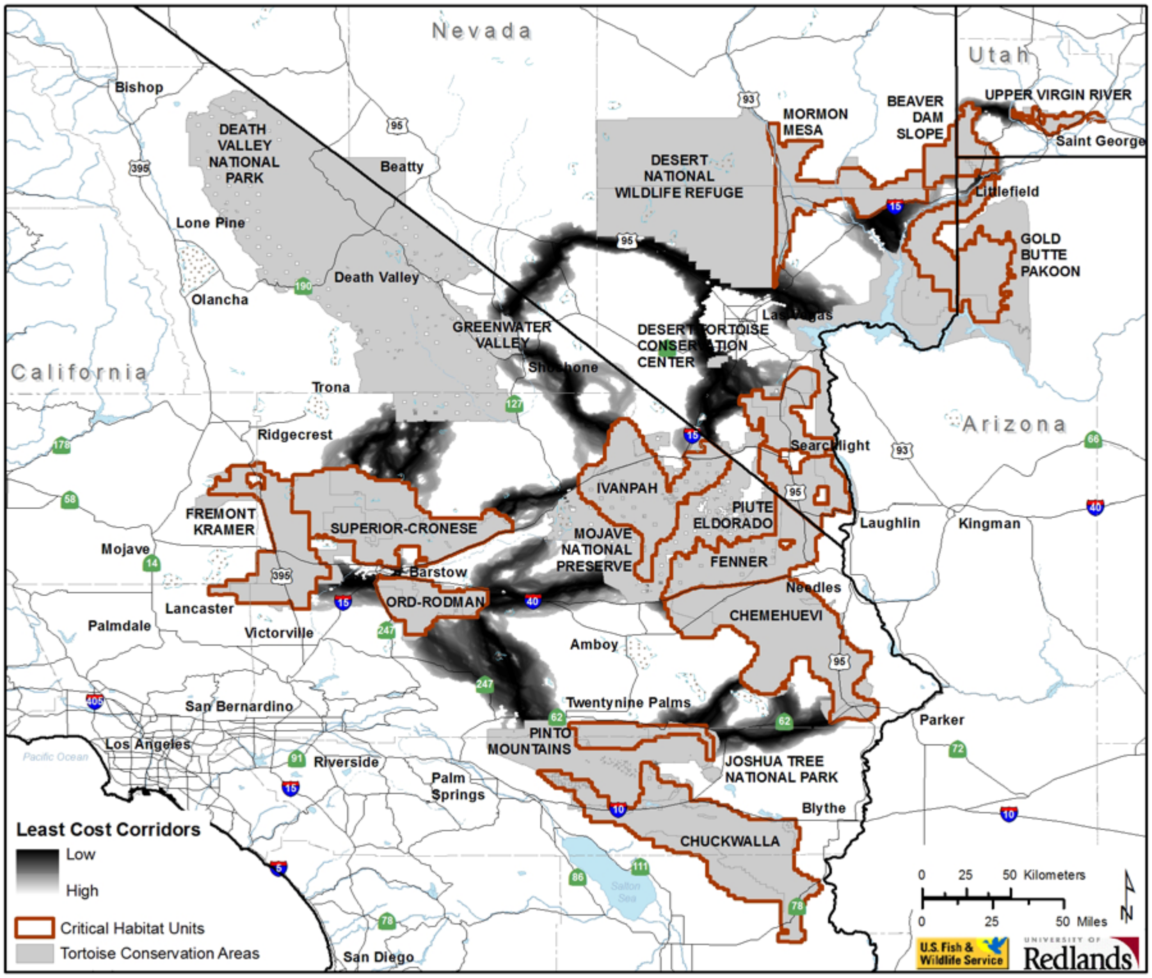

FIGURE 2. Least-cost corridors between tortoise conservation areas (Base model). Each corridor includes the lowest 1% cost-distance paths between tortoise conservation areas (TCAs), where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

function. The output of this series of operations was a raster of the corridor from/to each TCA polygon, which includes the lowest 1% cost paths from one TCA to another.

While overall movement resistance may be higher between two TCAs than between another pair, corridors between each TCA pair are important to population connectivity range-wide. Therefore, we normalized all corridors from 0–1 using a custom script written in Python. We also inverted these rescaled corridor values to represent importance for connectivity rather than cost.

We refer to the output from this process using the Suitable Habitat model as the "Base" model. The movement cost surface in the Base model assumes a 1:1 relationship between probability of tortoise occurrence in each pixel and resistance to connectivity. However, a

TABLE 2. Overlap (km^2, %) of Mojave Desert Tortoise (*Gopherus agassizii*) habitat in four least-cost corridor models with Department of Defense (DOD) lands, designated open off-highway-vehicle (OHV) recreation areas, and designated wilderness areas or Bureau of Land Management National Conservation Areas (NCAs).

	DOD	OHV	Wilderness/NCA
Base	2,375 (13%)	875 (5%)	2,952 (17%)
Base2	0 --	0 --	4,260 (26%)
Binned	7,165 (16%)	1,200 (3%)	6,985 (16%)
Binned2	0 --	0 --	7,145 (20%)

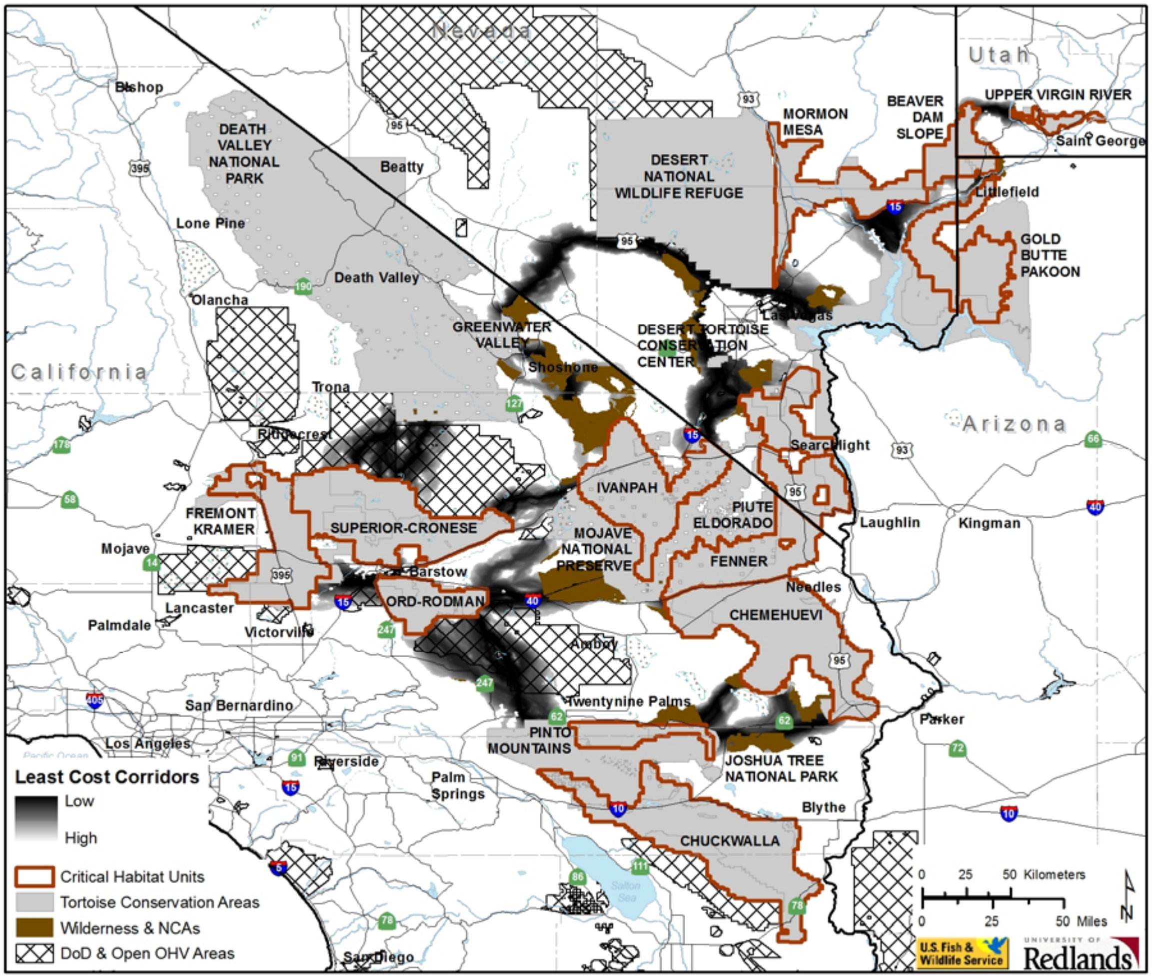

FIGURE 3. Least-cost corridors between tortoise conservation areas (TCAs; Base model), overlaid with Department of Defense (DoD) lands and open off-highway vehicle (OHV) areas, and showing designated wilderness areas and National Conservation Areas (NCAs) clipped to the linkages. Each corridor includes the lowest 1% cost-distance paths between TCAs, where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

pixel of moderate probability (e.g., 0.7) may contribute equally to connectivity as a pixel of high probability (0.9) if both pixels allow some degree of population presence or individual movement, especially at a temporal scale of a tortoise generation (about 25 y). For example, 95% of cells with known presence in the USGS habitat model had scores greater than 0.7 (Nussear et al. 2009). Therefore, we compared the Base model to a "Binned" model in order to evaluate uncertainty in our choice of resistance values, as recommended by Beier et al. (2009) and Sawyer et al. (2011). We developed the cost surface for the Binned model by re-scoring all pixels ≥ 0.7 in the Base model to 1.0, values 0.50–0.69 to 0.6, values 0.10–0.49 to 0.3, and values < 0.1 to 0. Other land uses also may affect desert tortoise connectivity, but are not captured by NLCD's developed areas of The Nature Conservancy's highly converted areas. Military training maneuvers and open-access off- highway-vehicle (OHV) recreation are high-impact activities that limit tortoise abundance, especially in the long term with increasing use (Bury and Luckenbach 2002; Berry et al. 2006). Therefore, we assessed effects on linkages of converting all Department of Defense (DOD) lands and open OHV areas to 0 habitat probability (models "Base2" and "Binned2").

RESULTS

Suitable Habitat (i.e., current estimated habitat) for the Mojave Desert Tortoise totals 67,000 km^2, 81% of the historic (i.e., unmanipulated USGS habitat model) estimated total of 83,138 km^2. The area of Suitable Habitat within TCAs, including areas of overlap with DOD lands, is 45,340 km^2 (68% of total current, 55% of total historic). Suitable Habitat within linkages connecting the TCAs in the Base model totals17,831 km^2

TABLE 3. Percentage overlap of least-cost corridors based on four connectivity models between Mojave Desert Tortoise (*Gopherus agassizii*) conservation areas. Total habitat area within each linkage is given along the diagonal.

	Base	Base2	Binned	Binned2
Base	17,831 km^2	81%	38%	35%
Base2	74%	16,282 km^2	34%	41%
Binned	92%	90%	43,597 km^2	97%
Binned2	70%	90%	79%	35,629 km^2

(27% current, 21% historic; Fig. 2). Several linkages are already severely constrained or impacted by DOD and open OHV area designations (Fig. 3, Table 2). Military training operations or high-intensity OHV recreation affect up to 18% of Suitable Habitat within linkages in the Base model. On the other hand, portions of some linkages (17%) are protected by wilderness or U.S. Bureau of Land Management (BLM) National Conservation Area (NCA) designations (Fig. 3, Table 2).

The Binned model had the effect of greatly lowering the resistance to tortoise occupancy, thereby increasing the amount of area included in the lowest 1% cost paths between TCAs (Fig. 4). Linkages in the Base model included only 38% of Suitable Habitat in the Binned model, while the Binned linkages included 92% of Base linkage habitat (Table 3). The total area of habitat within

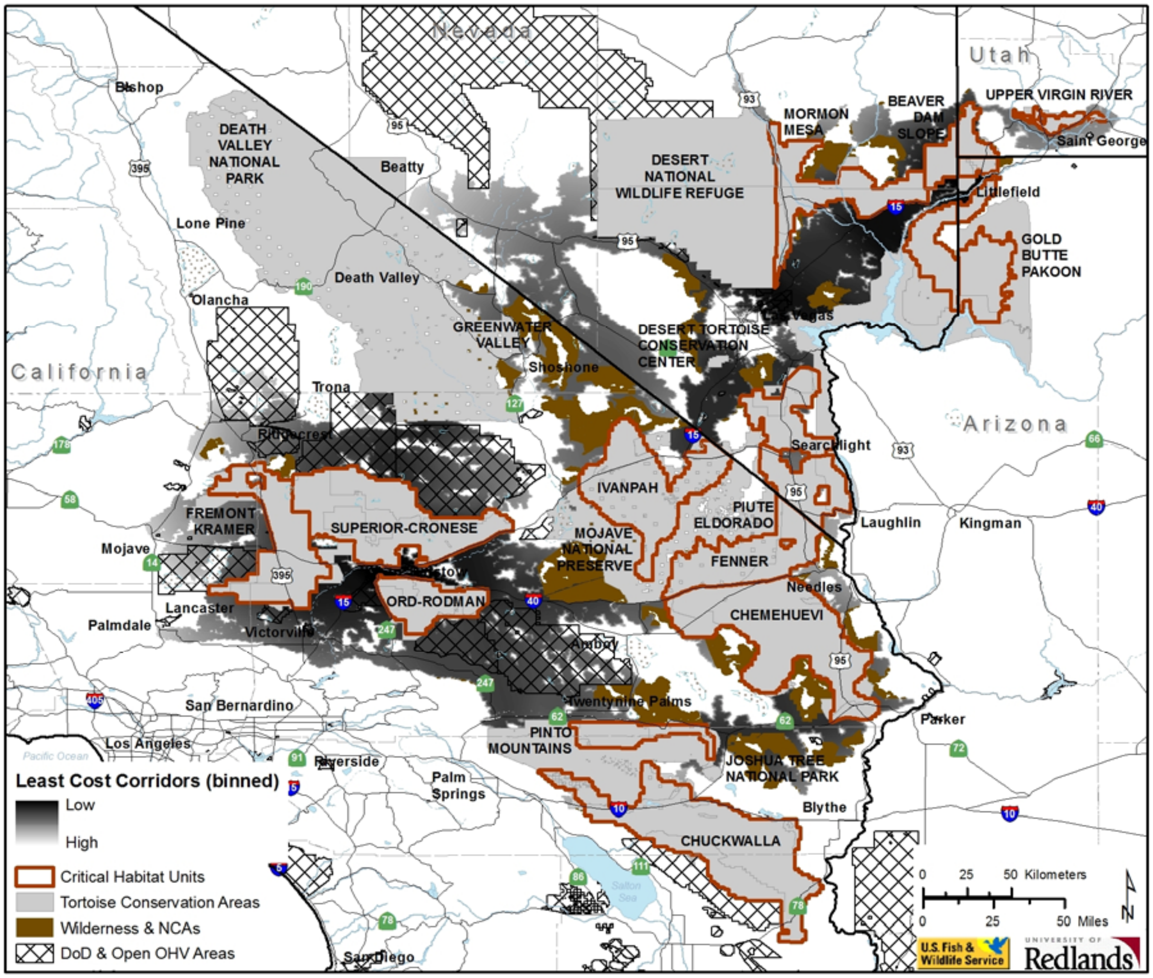

FIGURE 4. Binned model: least-cost corridors between tortoise conservation areas (TCAs), overlaid with Department of Defense (DoD) lands and open off-highway vehicle (OHV) areas, and showing designated wilderness areas and National Conservation Areas (NCAs) clipped to the linkages. Each corridor includes the lowest 1% cost-distance paths between TCAs, where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

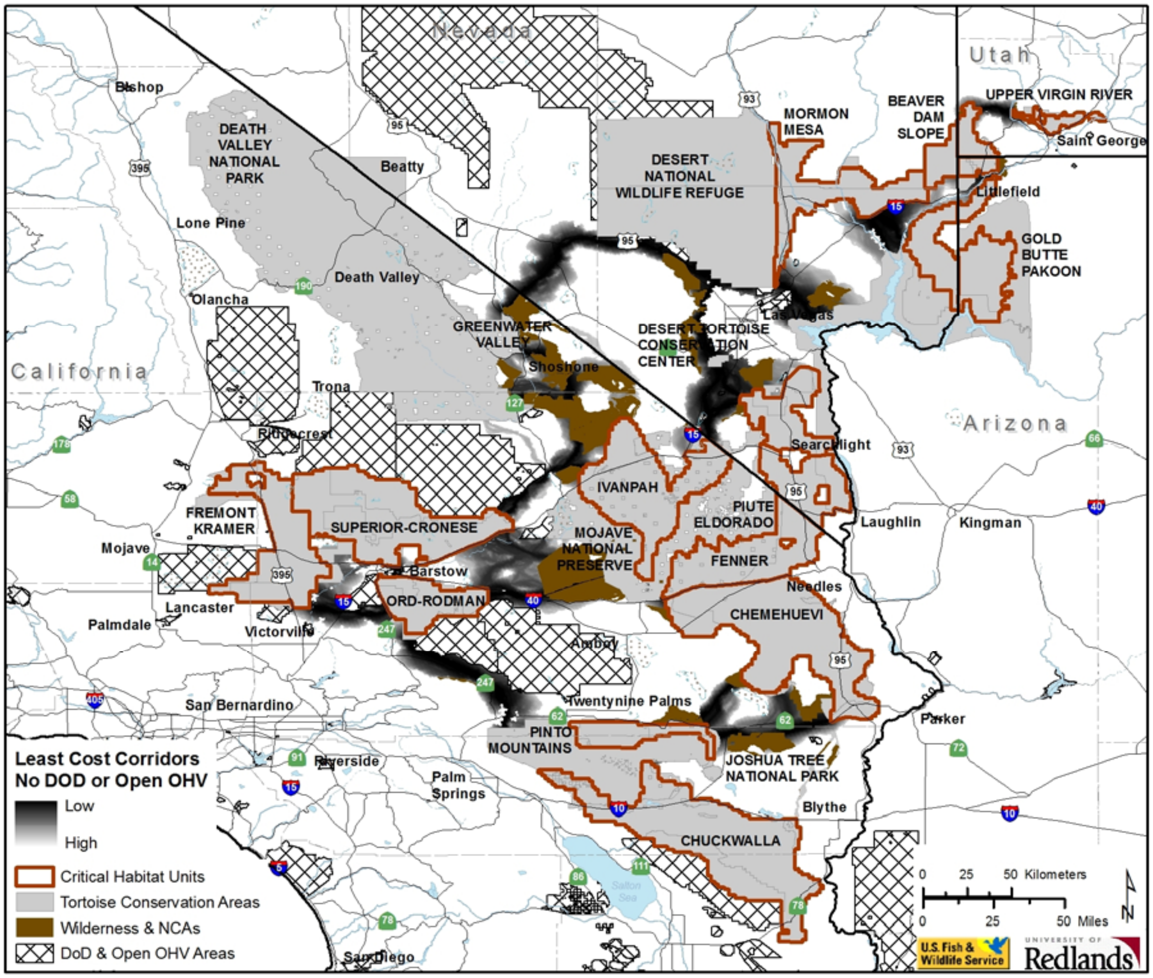

FIGURE 5. Base2 model: least-cost corridors between tortoise conservation areas (TCAs), overlaid with Department of Defense (DoD) lands and open off-highway vehicle (OHV) areas, and showing designated wilderness areas and National Conservation Areas (NCAs) clipped to the linkages. Each corridor includes the lowest 1% cost-distance paths between TCAs, where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

linkages in the Binned model totals 43,597 km^2 (65% current, 52% historic). Military training operations or high-intensity OHV recreation affect 19% of habitat within the linkages in the Binned model (Table 2). Current wilderness or NCA designations protect 16% of linkages in the Binned model (Table 2).

Excluding DOD and OHV designations from the cost surface reduced total habitat areas by 8.7% and 18.3% in the Base2 and Binned2 models, respectively (Table 3), although a greater proportion of the linkages is protected by existing wilderness or NCA designations (Table 2). Excluding these areas resulted in expansion of remaining linkages between TCAs, especially in California in the Base2 model (Figs. 5,,6). Overall, linkages in the Base model overlapped 81% of Suitable Habitat in the Base2 model, while the Binned model included 97% of Suitable Habitat in the Binned2 model (Table 3). Differences from 100% in proportion of habitat in the Base and Binned models that overlap the smaller Base2 and Binned2 models reflect shifts in the 1% cost surfaces. For example, in the Base2 model more of the area east of the Ord-Rodman and Superior-Cronese critical habitat units was important for connectivity, and new linkage strands were identified between the Chemehuevi and Chuckwalla critical habitat units (Fig. 5).

DISCUSSION

Successfully conserving the Mojave Desert Tortoise will entail managing not just conservation areas alone, but also the connections between these areas (i.e., managing the matrix between reserves: Fahrig 2001; Prevedello and Vieira 2010). Some TCAs are contiguous with others and together may contain viable

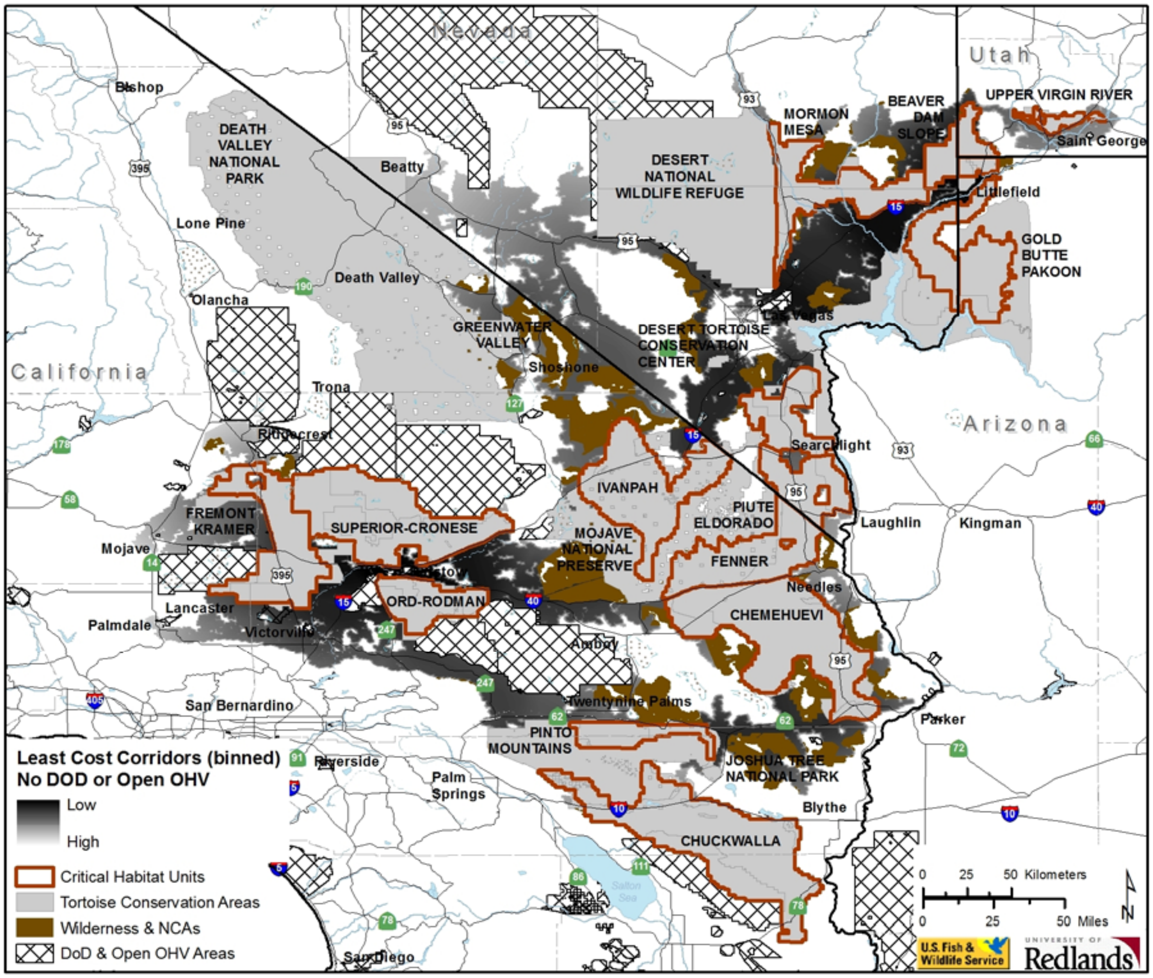

FIGURE 6. Binned2 model: least-cost corridors between tortoise conservation areas (TCAs), overlaid with Department of Defense (DoD) lands and open off-highway vehicle (OHV) areas, and showing designated wilderness areas and National Conservation Areas (NCAs) clipped to the linkages. Each corridor includes the lowest 1% cost-distance paths between TCAs, where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

numbers of desert tortoises, but even these contiguous blocks are adjacent to smaller, more isolated TCAs. Therefore, the function of the collective TCA network could be solidified by ensuring that all remain connected. In cases where much of the matrix between reserves remains undeveloped, managing the matrix to increase permeability and occupancy will be easier than restoring corridors after development has occurred (Prugh et al. 2008; Prededello and Vieira 2010).

In addition, most wildlife, including the Mojave Desert Tortoise, does not occur at uniform densities across landscapes (Krzysik 2002). The extent to which populations may fluctuate asynchronously, such as localized declines attributed to drought or predation events (Peterson 1994; Longshore et al. 2003; see also the model of recruitment in chaotic environments in Morafka 1994) even within designated conservation areas, increases risks to population viability and places increased emphasis on preserving population connectivity through the surrounding habitat matrix. Even under an assumption that TCAs are source habitats surrounded by sinks, maintaining or improving conditions within sinks/linkages can be as important to regional viability as protecting source TCAs because of their effect on neighboring source habitat (Carroll et al. 2003). Consequently, the effectiveness of TCAs will be improved if they are connected with functional habitat to ensure desert tortoise population persistence (U.S. Fish and Wildlife Service 1994, 2011). Ideally, linkages between TCAs would also be wide enough to buffer against detrimental edge effects (Beier et al. 2008), a recommendation applicable also to the TCAs, themselves (U.S. Fish and Wildlife Service 1994).

While specific management is needed within TCAs, these areas provide only an initial framework upon which to focus recovery efforts, especially given uncertainties related to the effects of climate change on Mojave Desert Tortoise populations and distribution (Barrows et al. 2011; U.S. Fish and Wildlife Service 2011). Temperatures are projected to change relatively quickly within desert ecosystems. To keep pace with changes from current temperature regimes within the current century, desert wildlife populations or species would need to shift their distributions at approximately 0.7 km/year (Loarie et al. 2009). At this rate, the current climate would cross each critical habitat unit (ranging in latitudinal extent of approximately 33–267 km) within 23–187 years. Notwithstanding potential elevational shifts by tortoise populations in response to climate change, which may be constrained in many areas as a result of geologic limitations on burrow construction, preserving connectivity between TCAs may allow shifts in the species' distribution and allow for future flexibility in refocusing management to ensure long-term recovery (Crooks and Sanjayan 2006; Krosby et al. 2010).

Connectivity conservation also is integral to maintaining genetic variability and ecological heterogeneity within and among populations of widely distributed species. Genetic analyses suggest that, historically, levels of gene flow among subpopulations of the Mojave Desert Tortoise were high, corresponding to high levels of habitat connectivity (Murphy et al. 2007; Hagerty 2008). All recent genetic studies of the Mojave Desert Tortoise have suggested that its population structure is characterized by isolation-by-distance; populations at the farthest extremes of the distribution are most differentiated, but a gradient of genetic differentiation occurs between those populations across the range (Britten et al. 1997; Murphy et al. 2007; Hagerty and Tracy 2010). This isolation-by-distance genetic structure across the relatively continuous historic distribution of the Mojave Desert Tortoise (Germano et al. 1994; Nussear et al. 2009) indicates that gene flow generally occurs (or historically occurred) according to a continuous-distribution model (Allendorf and Luikart 2007), as opposed to a metapopulation or stepping-stone model where individual tortoises move from one patch of suitable habitat across less suitable or non-habitat to another patch of suitable habitat.

Our modeling approach was similar to that of Hagerty et al. (2011), who modeled historic gene flow between populations across the range of the species across a cost surface based on the original (historic) USGS habitat model. Gene flow historically occurred in a diffuse pattern across the landscape unless otherwise constrained to more narrow, concentrated pathways created by topographic barriers (e.g., around the Spring Mountains in southern Nevada; Hagerty et al. 2011). Linkages between conservation areas are needed to conserve historic genetic gradation, thereby preventing habitat specialization and genetic divergence between populations (Frankham 2006). Where gene flow is constrained by topographic barriers, conservation of such concentrated pathways or linkages is especially important.

For gene flow to reliably occur across the range, and for populations within existing conservation areas to be buffered against detrimental effects of low numbers or density, populations need to be connected by areas of habitat occupied by tortoises. Low levels of genetic differentiation in Mojave Desert Tortoises have been detected across even relatively recent and narrow anthropogenic impacts on the landscape (Latch et al. 2011). Pairs of tortoises from opposite sides of a road exhibited significantly greater genetic differentiation than pairs from the same side of a road (Latch et al. 2011), raising even greater concerns for population fragmentation from larger scale habitat loss.

Assumptions and limitations.—Our assessment of important areas within which to preserve connectivity of Mojave Desert Tortoise populations is limited by shortcomings in our knowledge. We assumed that potential tortoise occupancy was accurately reflected by the USGS habitat model, as modified by our interpretation of the altered-habitat datasets, and that linkages of high-probability habitat between existing TCAs will help sustain viable populations across the range of the species. Implicit in this assumption is that various land uses or impacts occurring on the landscape (e.g., unpaved roads, exotic plant invasions) that were not explicitly included in the geospatial data we used do not impede connectivity of tortoise populations. We evaluated the effect of this assumption relative to large-scale potential impacts of high-intensity land uses (military training maneuvers and open OHV recreation), and additional areas emerged that may be important to connectivity.

Least-cost path analyses provide only a snapshot of current habitat conditions and are uninformative about demographic processes or how individuals actually move through a landscape (Noss and Daly 2006; Taylor et al. 2006). We assumed that a 1% cost surface would identify linkages wide enough to provide functional connectivity between TCAs. However, application of different resistance values from the underlying habitat model greatly influenced the total area and configuration of the 1% cost surface.

Indeed, limiting the cost surface to the lowest 1% is an arbitrary choice (Sawyer et al. 2011). The mean model score for all cells with known tortoise presence in the USGS habitat model was 0.84, and 95% of cells with known presence had scores greater than 0.7 (Nussear et al. 2009). Therefore, connectivity between tortoise populations (TCAs) may occur more broadly than estimated in the Base model. The more permeable Binned model identified linkages 245% larger in area than those in the Base model, while the linkages in the Binned2 model were 219% larger than those in the Base2 model.

Limited guidance is available for determining precise linkage widths, but minimum widths for corridor dwellers such as the Mojave Desert Tortoise should be substantially larger than a home range diameter (Beier et al. 2008). Inevitably, however, questions will be asked about what is the minimum width for a particular desert tortoise linkage, what is the relevant home range size from which to estimate that minimum width, and what are the minimum sampling considerations in estimating home ranges (cf. Harless et al. 2010). We agree with Beier et al. (2008) that this is analogous to asking an engineer, “what are the fewest number of rivets that might keep this wing on the airplane?” A more appropriate question for conservation is “what is the narrowest width that is not likely to be regretted after the adjacent area is converted to human use?” Managers and policy-makers must realize that conservation is not primarily a set-aside issue that can be dealt with by reserving a minimal percentage or amount of the landscape; rather, it is a pervasive issue that must be considered across the entire landscape (Franklin and Lindenmayer 2009).

Management implications and recommendations.— In general, land and wildlife managers should think about "corridors" between conservation areas that are large enough for resident tortoises to persist and to continue to interact with their neighbors within and outside broad habitat linkages, rather than expect that a more narrow band of habitat will allow an individual tortoise to move through it to the other side, breed with a tortoise on that side, and produce viable offspring that contribute to the next generation. Linkage integrity with sufficient habitat to support sustainable populations is important for Mojave Desert Tortoises and other corridor dwellers to support connectivity between core reserves (cf. Barrows et al. 2011). Given the underlying geospatial data, linkages in the Base2 model illustrate a minimum connection of habitat for Mojave Desert Tortoises between TCA pairs and therefore represent priority areas for conservation of population connectivity. However, large areas within these linkages are at risk of permanent habitat loss as a result of solar energy development.

Utility-scale solar development will require 831 km^2 of land by 2030 to meet the reasonably foreseeable development scenario within the entire states of California and Nevada (U.S. Bureau of Land Management and U.S. Department of Energy 2012). To meet this need, BLM has identified 39,830 km^2 of potentially developable public lands throughout these states (not all within Mojave Desert Tortoise habitat), including 866 km^2 of proposed solar energy zones (SEZs) within which solar energy production would be prioritized and facilitated. Meanwhile, projects totaling 190 km^2 and 1,470 km^2 had already been approved or were pending, respectively, across BLM land within the range of the Mojave Desert Tortoise (U.S. Bureau of Land Management and U.S. Department of Energy 2012). Relatively little linkage area would be consumed by the proposed SEZs (40 km^2), but 37 km^2 of approved and 703 km^2 of pending projects overlap linkages in the Base2 model, with some linkages at particular risk (Fig. 7). Even though substantial uncertainty surrounds the ultimate development footprint of pending solar development projects (or other proposed projects, including wind energy development), a separate analysis found that between 2,000 km^2 and 7,400 km^2 of lower conservation value land could meet California’s renewable energy goal by up to seven times over (Cameron et al. 2012). This suggests that renewable energy goals can be met without compromising the conservation of important Mojave Desert Tortoise habitat.

The Binned2 model includes blocks of contiguous habitat outside the Base2 linkage network, and many such areas likely contain substantial numbers of Mojave Desert Tortoises. Managers should consider additional conservation of occupied habitat adjacent to the Base2 linkages and existing TCAs to provide security against edge effects and population declines, especially given limitations previously identified in the existing reserve architecture. For example, even though use of DOD lands may be subject to change depending on national security needs, the value of military lands to conservation has long been recognized (Stein et al. 2008), and DOD-managed habitat that is unaffected by military training operations adds to the conservation base. Of additional note are blocks of habitat at the northern extent of the Mojave Desert Tortoise’s range, which may be of particular relevance for additional evaluation to determine more precisely how the modeled linkages will accommodate climate change (Beier et al. 2008).

Application of models from this study will require refinement at the local level and at a higher-resolution scale than the available geospatial data (i.e., finer resolution than 1 km^2) to account for on-the-ground limitations to tortoise occupancy and movement either not reflected in the geospatial data used here or as a result of errors in the land cover data we used to identify Suitable Habitat (Beier et al. 2009). For example, habitat connections through the northern end and across the boundary of the Chuckwalla critical habitat unit may be more limited by rugged topography than suggested by Figure 1 (Jody Fraser and Pete Sorensen, pers. comm.),

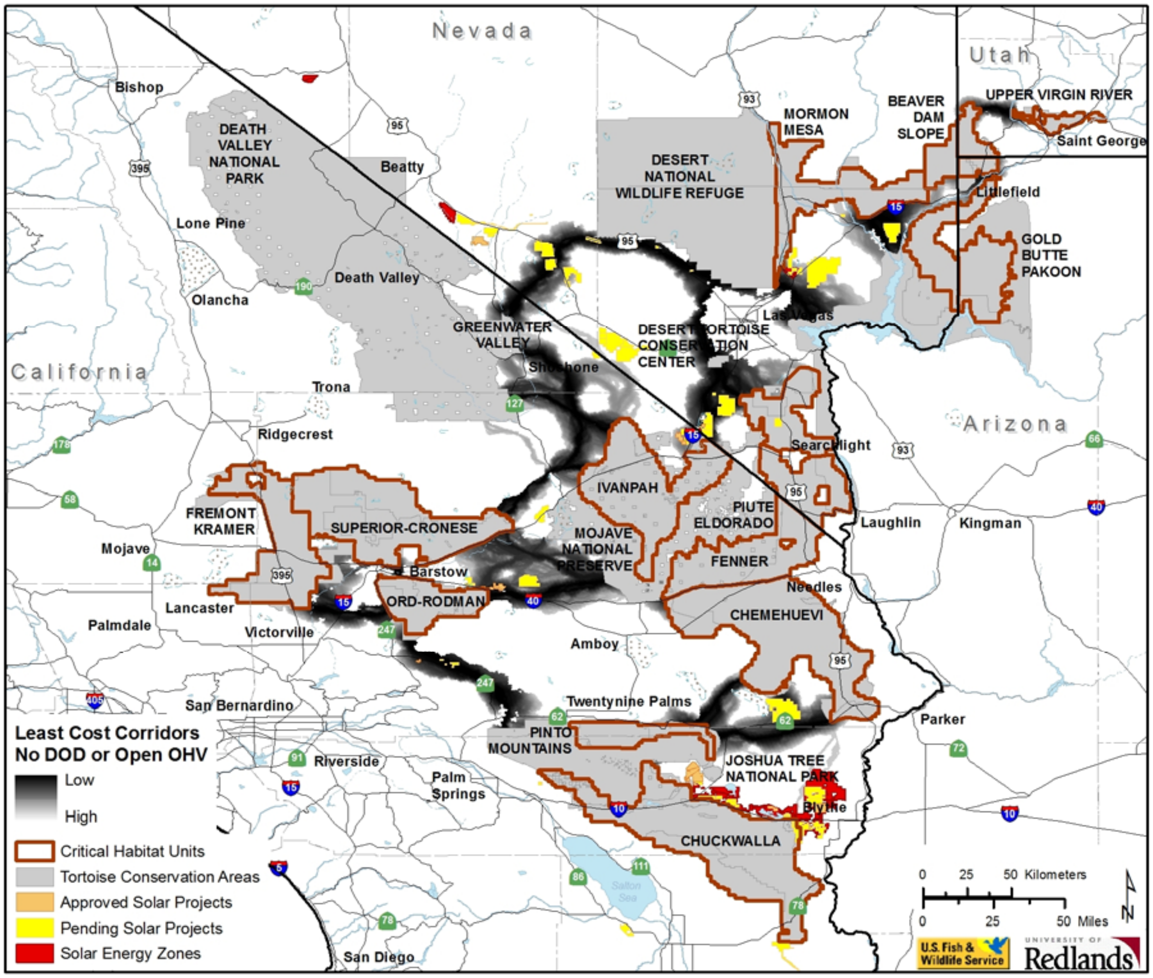

FIGURE 7. Least-cost corridors (Base2 model) between tortoise conservation areas (TCAs) relative to approved solar development projects, pending solar development projects, and solar energy zones. Each corridor includes the lowest 1% cost-distance paths between TCAs, where the relative cost to tortoises increases from black to white. White patterns within TCAs are private inholdings within federal lands.

thereby placing greater potential importance on the linkage identified on the north end of the critical habitat unit in the Binned2 model. In addition, more detailed or spatially explicit population viability analyses based on regional population and distribution patterns are needed to evaluate the ability of a conservation network such as that modeled here to ensure long-term persistence of Mojave Desert Tortoise populations (U.S. Fish and Wildlife Service 2011; e.g., Carroll et al. 2003).

While there is much still to be learned about the science and application of connectivity, land managers cannot wait for research to resolve all relevant questions before focusing effort on enhancing connectivity. Instead, science and management must proceed in parallel with the flexibility to modify future management in the light of new knowledge (Lovejoy 2006). In areas proposed for essentially permanent habitat conversion, such as by large-scale development, there is the risk that critical linkages will be severed before they are protected (Morrison and Reynolds 2006). For species with long generation times like the Mojave Desert Tortoise, this risk is compounded by the fact that we are not likely to detect a problem with a population until well after we have reduced the habitat below its extinction threshold (Fahrig 2001).

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Research Article

Identifying Habitat Linkages to Maintain Connectivity for Corridor Dwellers in a Fragmented Landscape

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ABSTRACT Anthropogenic habitat fragmentation typically precedes conservation planning; maintaining remaining linkages among core habitat areas can thus become a key conservation objective. Identifying linkages for dispersal and ensuring those linkages have long-term protection and management are challenging tasks for wildlife managers. These tasks can be especially daunting for smaller species with low mobility, termed corridor dwellers, which must maintain sustainable populations within corridors. Between May 2007 and June 2009, we collected occurrence locations for a corridor dweller, the Palm Springs pocket mouse (*Perognathus longimembris bangsii*), from museums, previous research, and our own field sampling. We used those data to model their suitable niche space and then identify suitable linkages between proposed conservation areas. We used a partitioned Mahalanobis D^2 statistic to create a spatially explicit niche model describing the distribution of a suitable niche space, and we validated the model statistically, with live trapping and with burrowing owl (*Athene cunnicularia*) diets. Our model identified soil characteristics, topographic ruggedness, and vegetation as variables delimiting Palm Springs pocket mouse habitat; sand content of the soils was an especially important characteristic. Our historic distribution model identified 120,000–90,000 ha as historically potential Palm Springs pocket mouse habitat; roughly 39% of that has been lost to more recent development. Most of the remaining suitable habitat occurred in the northwestern portion of the valley. We modeled habitat within core reserves as well as within proposed linkages between those reserves as having high similarity to known occupied habitats. Live trapping in areas with high (≥ 0.95) Habitat Suitability Index (HSI) values resulted in captures at 66% of those locations and, along with burrowing owl diets, refined a qualitative model as to what constituted a suitable Palm Springs pocket mouse corridor. While most corridor analyses have focused on mobile species which may traverse corridors in hours, days, or weeks, linkages for corridor dwellers must include habitat for sustaining multi-generational populations. This requires evaluating whether continuous suitable habitat exists within proposed corridors. Our research demonstrates how niche modeling can provide a landscape-scale view of the distribution of suitable habitat to evaluate conservation objectives for connectivity.

KEY WORDS Coachella Valley, conservation, corridor dwellers, linkage, Mahalanobis D^2, niche model, Palm Springs pocket mouse, *Perognathus longimembris bangsii*, suitable niche space.

Creating reserves for sustaining species' populations and natural community associations is a cornerstone of conservation strategies (Meir et al. 2004). Fragmented landscapes may include a high diversity of species but favor weedy and invasive species, which may out-compete those more sensitive to area or habitat quality; creating carefully designed, large reserve networks across a landscape can accommodate the requirements of those more sensitive species (Noss and Cooperrider 1994). One of the challenges for creating reserve networks is maintaining connectivity between reserves for facilitating gene flow, avoiding demographic bottlenecks, and allowing species to track shifts in their habitat in response to climate change (Beier et al. 2008). The term "corridor" is generally defined as a "broad, internally heterogeneous swath of habitat that permits or directs the spread of taxa from one region to another" (Noss 1991:27). When a corridor that provides movement for species also includes ecosystem and community processes that support smaller animals for dispersal over multiple generations, the corridor is also known as a linkage (Csuti 1991). Ensuring such linkages protect long distance dispersal conduits for plants, reptiles, amphibians, and small mammals between core habitat patches, assisting with metapopulation persistence over multiple generations, is a challenge (Noss and

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Cooperrider 1994). Unlike more mobile species, which may traverse corridors in hours, days, or weeks, linkages for less mobile species must include habitat for sustaining multi-generational populations; such species are termed corridor dwellers (Beier et al. 2008:844).

Small mammals are examples of corridor dwellers as they often have relatively small home ranges and dispersal abilities (Price et al. 1994). Previous empirical corridor studies with small mammals have been conducted in fragmented forest environments (Bennett 1990, Bennett et al. 1994, Downes et al. 1997, Bowman and Fahrig 2002, Mabry and Barrett 2002). Bennett (1990) documented the use and critical importance of habitat patch size within corridors for small mammals in Australia both as means for dispersal and as multigenerational gene flow through residents. Here we present a corridor suitability analysis for an arid lands corridor dweller, the little pocket mouse (*Perognathus longimembris*), a species restricted to fine sandy soils throughout its distribution (Jameson and Peeters 1988, Penrod et al. 2005; S. C. Dodd, Coachella Valley Association of Governments 1996, unpublished report). That edaphic constraint and the disjunct distribution of those soils have likely contributed to the high degree of taxonomic divergence leading to as many as 23 named subspecies throughout the western United States (McKnight 2005). Several of those subspecies occurring in southern California have been important elements of regional conservation planning efforts where reserve connectivity is a key plan component (e.g., Dudek 2003, 2007).

Within the confines of southern California's Coachella Valley, the little pocket mouse subspecies is generally accepted as the Palm Springs pocket mouse (*P. l. bangsi*), although genetic analyses indicate complex genetic affinities there (Swei et al. 2003, McKnight 2005). Palm Springs pocket mice have been classified as a species of special concern by the state of California due to habitat degradation and to fragmentation by urban, residential, and agricultural development (California Department of Fish and Game [CDFG] 1994, Swei et al. 2003, Coachella Valley Association of Governments [CVAG] 2006). The pocket mouse is one of 27 focal species in the Coachella Valley Multiple Species Habitat Conservation and Natural Community Conservation Plan (Dudek 2007). One of the explicit objectives of the Coachella Valley conservation program is to maintain current connectivity among identified core reserves for each species. In response to that objective we modeled habitat for the Palm Springs pocket mouse to determine the extent to which suitable habitat for this species still occurs between core reserve areas and to provide an indication of the potential for occupancy within those corridors.

Wildlife corridors and their utility is a much debated topic in conservation biology (Simberloff and Cox 1987, Noss 1987, Hobbs 1992, Hess 1994, Lindenmayer and Fischer 2006, Beier et al. 2008). The debate is not whether connectivity is important to population sustainability, but whether given linkages function to provide connectivity for specific species or ecological processes. Characteristics often associated with typical wildlife corridors may work against their ability to meet conservation and management objectives; high road density, invasive species access, predation, increased edge effects, and human activity all degrade the functionality of the linkage (Noss and Cooperrider 1994). Unless connectivity between reserves is well designed and managed corridors between reserves may offer more threats and hazards than opportunity; the narrower and more limited the habitat in the corridor, the higher the probability that species will be affected by predation, edge effects, and the negative effects of roads and other anthropogenic barriers (Noss 1991).

The challenge of securing habitat connectivity is exacerbated because conservation planning typically does not begin until after substantial landscape fragmentation has already occurred. Conservation planners need tools for identifying if and where potential linkages for these less mobile corridor dwellers occur, as well as for identifying landscape characteristics that support or compromise their population sustainability within those corridors. Our assumption for Palm Springs pocket mice as corridor dwellers simplifies corridor identification; linkages must include suitable habitat and area sufficient to sustain a population. For corridor dwellers the requirement for sufficient within-corridor habitat to support a sustainable population highlights the importance of corridor integrity to support connectivity between core reserves.

Modeling a species' suitable habitat begins with identifying variables that constrain its distribution across a heterogeneous landscape (Rotenberry et al. 2002, 2006). There are 2 main categories of modeling approaches prevalent in conservation: 1) ecological niche modeling (ENM) and 2) least-cost path (LCP) analysis (Pinto and Keitt 2009). Ecological niche modeling employs multiple Geographic Information System (GIS) linked variables measured at known species locations and then statistically determines which combination of variables best describe mean conditions for the species' suitable habitat, or niche. Using GIS, maps of the distribution of that species' suitable habitat can be generated (Barrows et al. 2008, Waltari and Guralnick 2009). Least-cost path analyses also use GIS to identify a likely route of travel for the species by selection of a combination of environmental variables that represent the path of least resistance and the shortest distance between 2 patches of habitat (Li et al. 2010).

We chose ENM because it allowed us to model multiple dispersal routes across a heterogeneous landscape matrix. In practicality species will rarely choose just one optimum route, and species do not act in an optimal and predictive manner due to the availability of a path of least resistance (Pinto and Keitt 2009). Identifying habitat relationships allows us to model habitat available for a species and to describe potential current and historical distributions, leading to identifying sites most suitable for protection strategies (Barrows et al. 2008). Our objective here was to evaluate whether ENM can provide a landscape-scale view of the distribution of suitable habitat to evaluate conservation strategies for achieving species-specific connectivity.

STUDY AREA

Palm Springs pocket mice occur from the San Gorgonio Pass area east to the Little San Bernardino Mountains and south along the eastern edge of the Peninsular Ranges to Borrego Valley in southern California (Hall 1981). The Coachella Valley and the San Gorgonio Pass area contained about 90% of the Palm Springs pocket mouse range, including the western, northern, and eastern limits of its distribution. The southern portion of its range near Anza Borrego State Park fell outside the Coachella Valley Multiple Species Habitat Conservation Plan area (CVAG 2006).

Our study encompassed nearly 690,000 ha centered on the floor of the Coachella Valley of Riverside County, California, extending south to the county border and north into the western regions of Joshua Tree National Park (Fig. 1). The Coachella Valley is an extremely arid shrub desert with a mean annual rainfall of 79–125 mm (most recent 60 year means, Western Regional Climate Center, Palm Springs and Indio reporting stations). The lowest rainfall years occurred in 2002 and 2007, with just 3.6 mm and 4.4 mm recorded at our study site. Temperatures range from a low approaching 0° C in the winter to highs exceeding 45° C commonly recorded during July and August. Since 1980 this region has experienced a second home-golf resort development explosion, currently with an estimated 130 separate golf courses, numerous roads, railways, and suburban development fragmenting the remaining natural habitats of the valley floor.

With our species-specific definition of a suitable corridor (requiring sufficient habitat for occupancy) the separation of core versus corridor habitats becomes muddied. To avoid that confusion, we used the selection of 5 core areas, broad protected habitat areas deemed sufficient to provide for long-term sustainable populations, and their linkages for the pocket mouse as defined in the Coachella Valley Multiple Species Habitat Conservation Plan (CVMSHCP; Dudek 2007) and by others (S. C. Dodd, unpublished reports; R. James, United States Department of the Interior, Fish and Wildlife Service 1997, unpublished report): 1) The westernmost edge of the Coachella Valley and the Palm Springs pocket mouse's range (Windy Point—Snow Creek Preserve Unit); 2) north Palm Springs (Whitewater Floodplain Preserve); 3) south of Desert Hot Springs (Fault-line dunes—Willow Hole Preserve Unit); 4) northwest Desert Hot Springs (upper Mission Creek and Morongo Wash Preserve Unit); and 5) the easternmost core area for this species (Thousand Palms Preserve; Fig. 2).

METHODS

We collected historic data on Palm Springs pocket mice from a variety of sources including the University of California Museum of Vertebrate Zoology, California Academy of

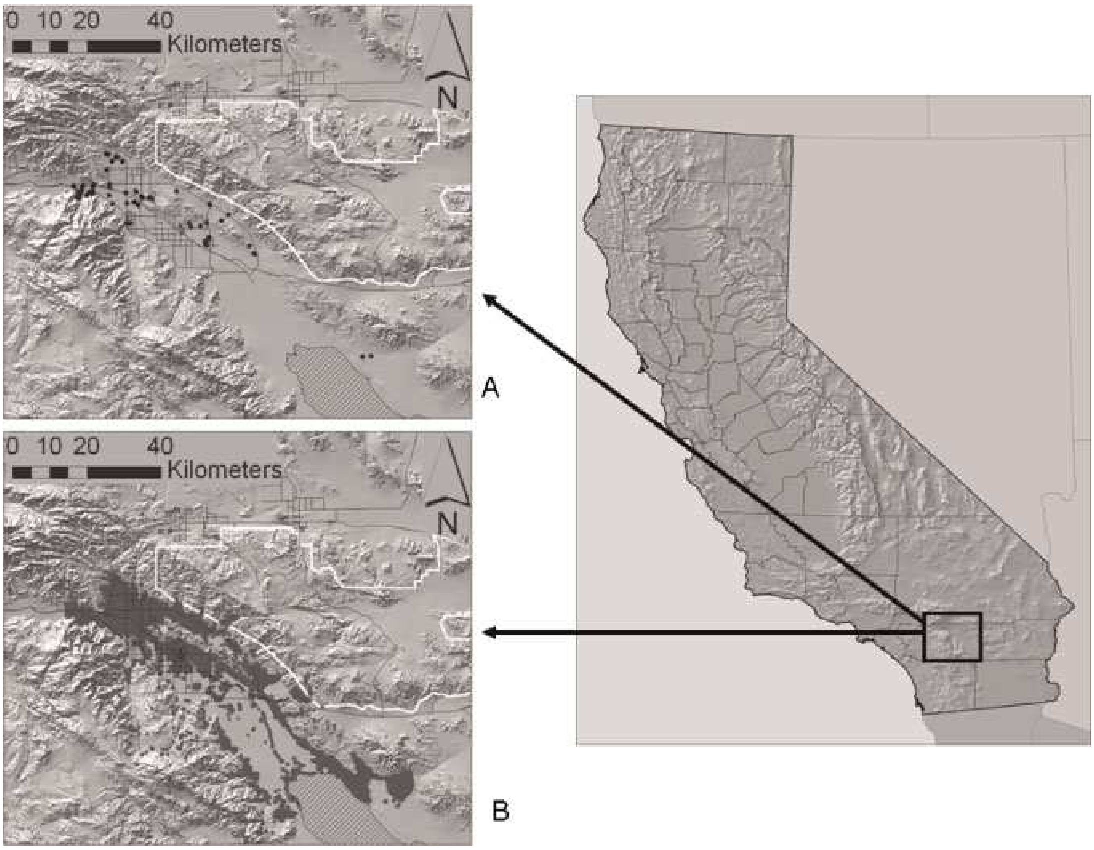

Figure 1. Our Coachella Valley study area with (A) distribution of Palm Springs pocket mouse locations we used to develop the Mahalanobis D^2 niche model, and (B) 2009 (dark gray shaded region) extent of modeled suitable habitat in the Coachella Valley. Area delineated with the white outline is Joshua Tree National Park boundary.

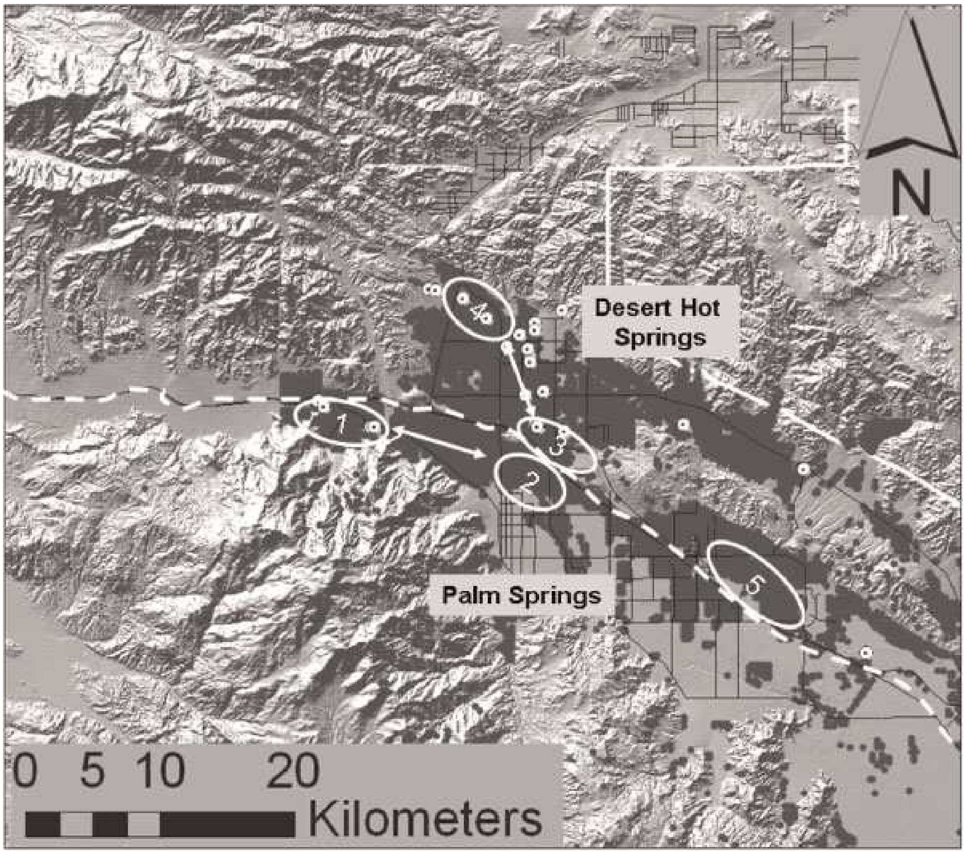

Figure 2. The extent in 2009 of modeled suitable habitat for the Palm Springs pocket mouse in the northwestern Coachella Valley. Core preserves established under the Coachella Valley Multiple Species Habitat Conservation Plan are identified by white ovals: 1) Windy Point—Snow Creek; 2) Whitewater Floodplain Preserve; 3) Fault-line dunes—Willow Hole; 4) upper Mission Creek and Morongo Wash channels; 5) Thousand Palms Preserve. White dots indicate where we verified presence of Palm Springs pocket mice with either live trapping or burrowing owl diet analyses. Dashed white line shows Interstate 10 as it bisects the Coachella Valley.

Sciences, and the California Natural Diversity Data Base of the California Department of Fish and Game. We georeferenced all museum locality records (specimens) and biologists' reports associated with surveys contracted for development of the CVMSHCP to as precise a location as possible; we did not include in our analysis those records whose descriptions did not allow us to define the locality identification with a precision of ≤180 m resolution, as we could not accurately assign those locations to the cell size we used in niche-habitat suitability modeling (see below). The location records documented species presence only and yielded 83 spatially nonredundant locations (i.e., locations ≥180 m apart) where ≥1 specimens were documented in past field surveys for the Palm Springs pocket mouse. We used these data (ranging from 1908 to 2009) to calibrate and validate the pocket mouse distribution model.

Niche Modeling

We used the Mahalanobis distance statistic (D^2; Clark et al. 1993; Rotenberry et al. 2002, 2006; Browning et al. 2005) to model the historical distribution and the currently available habitat. To distinguish between modeled habitat and habitat measured on the ground, we refer to the model output as suitable niche space. The Mahalanobis statistic has several advantages over other spatially explicit modeling approaches, the foremost being that only species presence data are required for the dependent variable. Because only positive occurrence data are required, we can use data from a range of disparate sources, including location records from museums, as long as there is sufficient precision to assign each observation to an individual cell used in the modeling process. Using only presence data also avoids the uncertain assumption of correctly identifying truly unoccupied habitats (Knick and Rotenberry 1998, Rotenberry et al. 2002, Browning et al. 2005).

We refined the Mahalanobis statistic by partitioning it into separate components (Dunn and Duncan 2000; Rotenberry et al. 2002, 2006). This partitioning is based on a principal components analysis of the selected model variables in the calibration data set. Each of the partitions is additive, orthogonal multivariate combinations that explain increasingly more variance until the final partition, the full model (labeled with the lowest partition number [1]), captures the full range of variance exhibited in the calibration data. The partition with the smallest eigenvalue, labeled with the highest partition number (equal to the number of variables being analyzed), is associated with the combination of habitat variables that have the least variation among locations, potentially indicating minimum habitat requirements. The assumption is that variables with low variance are more likely to represent essential attributes explaining a species' distribution than those that take on a wide range of values where a species is present. Modeling with variables that demonstrate the least variability may be appropriate for projecting potential shifts in distributions in changing environments as key habitat constraints would be held constant (Dunn and Duncan 2000; Rotenberry et al. 2002, 2006). We calculated Mahalanobis distances and their partitions with SAS code provided in Rotenberry et al. (2006).

Modeling procedure.– We uniformly divided the GIS map file of the study area into 211,949 180-m × 180-m cells. Cell size determines the scale at which the modeling results are relevant; we selected our cell size so that it roughly corresponded with a scale equal to 2–3 home ranges of a pocket mouse (Chew and Butterworth 1964, Maza et al. 1973) and thus indicated sufficient habitat for multiple individuals to reside within. A much smaller cell size could exclude the influence of variables potentially important to the occurrence of this species (such as roads, suburban, or agricultural development); a much larger cell size could include the influence of variables that would never be encountered by a pocket mouse (features well beyond the home range of this species). We scored each cell for the underlying environmental variables. We extracted cells that contained a species' observation to create the calibration data set from which we created a species' habitat model using a SAS script provided by Rotenberry et al. (2006). Once we created a model, we used it to calculate a Habitat Similarity Index (HSI) for each Mahalanobis distance partition for every cell on the map. Following Rotenberry et al. (2006), we rescaled each HSI to range from 0 to 1, with 0 being the most dissimilar and 1 being identical to the mean habitat characteristics of the Palm Springs pocket mouse based on the calibration data set. We used ArcGIS 9.1 (Environmental Systems Research Institute, Redlands, CA) to provide a spatial model (niche map) of the similarity to the species mean for each cell. We then overlaid these modeled areas with GIS layers for anthropogenic changes to the landscape that might render the historic habitat no longer suitable, such as large-scale agricultural and urban-suburban development, to derive an estimate of current suitable habitat availability.

The calibration data set was comprised of a random 60% (50 points) of the total spatially non-redundant location data (83 points). We employed validation data sets to select which of the model partitions created in the Mahalanobis niche-modeling process represented the most accurate model; we used the remaining 40% (33 points) of total data to independently validate the model we developed from the calibration data set. We calculated median HSI values for the validation points for each partition for each model (each combination of variables). We selected the model partition that yielded the highest median HSI values for the validation data set as the best performing model.

Habitat variables.– We selected habitat variables based on our expectation of their likely influence on the distribution of the Palm Springs pocket mouse, on our literature reviews, and on independence of those variables from anthropogenic change in the valley. To prevent model over fitting, we maintained a ratio of one variable per 10 observations (Osborne and Costello 2004). Because the calibration data set contained 50 non-redundant observations, we limited the number of variables to 5.

We constructed partitioned Mahalanobis D^2 models with different suites of abiotic variables. We derived all of the variables we used to model the pocket mouse from GIS layers readily available from internet sources in 2008; soils (Natural Resources Conservation Service 2008*a*, *b*); ruggedness (United States Geological Survey 2009); vegetation: (Davis et al. 1998); and climate (PRISM Climate Group 2004). Variables included metrics for mean climate (mean annual precipitation, mean high temperature in Jul, mean low temperature in Jan), change in elevation within a 3 × 3-cell neighborhood analysis using 10-m cells (ruggedness 3 × 3), change in elevation within a 18 × 18-cell neighborhood analysis using 10-m cells (ruggedness 18 × 18). The 2 ruggedness scales allowed us to interpret which scale was important for identifying pocket mice occupancy. Additional variables included broad soils categories such as percent sand and silt and vegetation type (Holland 1986) within each 180-m × 180-m cell.

Live Trapping

We conducted live trapping between May 2007 and June 2008 to evaluate model predictions of suitable niche space. Trapping data alone remain inadequate for assessing pocket mouse distribution (or potential distribution) due to several constraints. We were limited in the locations for our trapping to public access, public right-of-way, and existing conservation ownership. Because of these constraints, we could not randomly distribute trapping locations, so we focused our trapping to cover a broad range of potential occupation conditions that we could couple with modeling efforts at locations within the same core areas identified by the CVMSHCP (Dudek 2007) and by others (S. C. Dodd, unpublished report; R. James, unpublished report; Fig. 2). Within these core areas we randomly selected transects to test for presence–absence of the Palm Springs pocket mouse. We used 9 cm × 7.5 cm × 23-cm Sherman aluminum traps (H. B. Sherman Traps, Tallahassee, FL), each fitted with a large (5 cm) spring steel binder clip attached to the trap entrance to keep the door from closing snugly and thus eliminating tail damage to kangaroo rats (*Dipodomys* spp.) caught inadvertently. Each transect consisted of 4 clusters of 20 Sherman traps, with each cluster $\geq$250 m apart (for a total of 80 traps/transect). The 250-m spacing ensured each trapping grid occurred in separate 180-m × 180-m cells used in the construction of the niche models, providing non redundant location data for the development of those niche models. Additionally, this spacing allowed us to evaluate presence or absence within varying habitat, slope, and soil types. Within each cluster, we laid the 20 Sherman traps in a grid spacing commonly composed of 4 lines about 15 m apart. Each line comprised 5 traps each about 5 m apart (Chew and Butterworth 1964).

We baited each trap with organic dry rolled oats to prevent spread of exotic weed seeds sometimes associated with seed mixes. Trapping occurred only when evening temperatures were >15.5° C and when wind speeds were <33 km/hr to prevent inadvertent trap closure and episodes of torpor. We set all traps at or near dusk and then checked and collected them at or near midnight to reduce potential stress to trapped animals. Previous studies on this and similar species noted most nocturnal activity occurred between sunset and midnight, and spikes in seasonal activity and temperatures occurred in spring and autumn, during which we based our methods (Chew and Butterworth 1964; French 1977; S. C. Dodd, unpublished reports; R. James, unpublished report).

We marked individuals on the ear with a permanent ink marker (Sharpie®, Newell Rubbermaid, Freeport, IL) to identify recaptures on subsequent trap nights. Because our objective was to determine occupancy and not density, we trapped the same location for up to 3 successive nights or until we captured a Palm Springs pocket mouse, resulting in ≤240 total trap nights per transect. Once we captured a Palm Springs pocket mouse, trapping at that location ceased and moved to a new location. Because we never trapped beyond 3 nights on any transect, the Sharpie pen was sufficient in the arid environment to detect recaptures during our study. We chose this method over other common methods such as passive integrated transponder (PIT) tags and toe clipping due to the extremely small size of this species and the short duration of our study. For each captured animal we recorded weight, sex, age, and Universal Transverse Mercator (UTM) capture coordinate, as well as the time, temperature, and wind speed before we released the animal unharmed.

Because trapping at any one location was not exhaustive Palm Springs pocket mice may have been present at locations where we did not find them. However at locations where we found Palm Springs pocket mice, they were usually captured the first night of trapping. We based species identifications on diagnostic hind foot and ear measurements along with pelage color (Jameson and Peeters 1988). We conducted trapping under CDFG Permit (no. 008781) and a University of California Animal Use Permit (UC AUP Permit no. A-20070022) and followed American Society of Mammalogists preliminary guidelines for field work in Mammalogy (American Society of Mammalogists 1998).

Owl Pellet Analysis

In 2009 we collected regurgitated pellets from burrowing owls across the Coachella Valley as an ancillary pocket mouse trapping method, to provide both an additional validation test to our niche model as well as examine relationships with different anthropogenic landscape changes. Reported home ranges for burrowing owls yield mean distances from burrows to home range perimeters of 400–600 m, providing an estimate of how far from their burrows owls typically foraged (Haug and Oliphant 1990, Gervais et al. 2003, Rosenberg and Haley 2004). We walked linear transects that were aimed at determining presence of burrowing owls and their burrows, and collected pellets adjacent to those active burrows. We included in our analyses only those pellet collections with ≥10 pellets and ≥12 prey items. Pellet collection locations we categorized as agriculture, suburban (high density housing with few empty lots), suburban–wildland interface (scattered homes often on the margins of denser suburbia, with ≤2 homes/ha), or wildland (no occupied structures or altered habitat). We based identification of prey on comparisons of jawbones with specimens collected previously in our field studies.

RESULTS

The most parsimonious ENM model was determined by the variable combination with both the highest median HSI values for both the calibration and validation data sets; those variables included soil, vegetation, and topography variables: percent sand, percent clay, vegetation type, ruggedness 3 × 3, and ruggedness 18 × 18. We tried other variables, including mean maximum temperature in July, mean minimum temperature in January, average precipitation, and slope in multiple combinations with and without soils variables, but no variable combination performed as well as the soils–vegetation–ruggedness model. The best performing principle components partition was the fifth, the partition capturing variables that demonstrated the least variation among all the occupied cells. Within the fifth partition soils variables dominated with high percent sand and low percent silt characterizing the cells occupied by Palm Springs pocket mice (Table 1).

The high median HSI of the occupied cells we used for validation (Table 1) was an indication the ENM correctly identified cells with high suitable niche space for the Palm Springs pocket mouse. Within the 170,300-ha Coachella Valley floor our analysis resulted in a niche model that indicated that historically approximately 71% was suitable habitat with HSI values ≥0.5, 62% with HSI values ≥0.75, and 53% with HSI values ≥0.95. These values indicate the extent of suitable habitat prior to anthropogenic land cover changes. With anthropogenic landscape changes that have occurred across the Coachella Valley, current Palm Springs pocket mouse suitable niche space has been reduced by 34–40% on the valley floor (Table 2).

The ENM indicated most of the highest ranking habitat occurred historically as well as currently in the northern and western-most portions of the Coachella Valley (Fig. 1). The relative lack of modeled habitat with high suitability in the center of the valley corresponds to active aeolian sand dunes

Table 1. Niche model parameters for the Palm Springs pocket mouse as applied to the Coachella Valley of California, May 2007–June 2009.

Model parameters (independent variables)	**Values**[a]
% sand	0.7153
% clay	0.6925
Ruggedness 3 × 3	0.0884
Ruggedness 18 × 18	−0.0321
Vegetation type	−0.0013

[a] Eigenvalues for the principle component with the highest median Habitat Suitability Index value.

Table 2. Modeled areas for historic and current extent of suitable habitat for the Palm Springs pocket mouse in the Coachella Valley, California, 2009.

	Median HSI[a] $\geq$ 0.5	**Median HSI $\geq$ 0.75**	**Median HSI $\geq$ 0.95**
Historic extent of suitable habitat	120,380 ha	106,160 ha	90,240 ha
Current extent of suitable habitat	79,640 ha	64,080 ha	55,130 ha
% habitat loss	34%	40%	39%

[a] Habitat Suitability Index.

and the historic extent of Lake Cahuilla. A closer view of the northern–western portion of the Coachella Valley shows contiguous habitat still exists between 4 of the 5 proposed core habitat reserves in that region (Fig. 2). However, there are numerous roads, including an 8-lane interstate freeway, that compromise that connectivity.

Our live trapping resulted in positive Palm Springs pocket mouse captures at 66% of locations we trapped. Three areas yielded no captures (Fig. 2). The Dos Palmas Access Road was modeled to have lower and patchier habitat suitability. The locations at Indian Avenue and the Whitewater Floodplain Reserve were among the windiest locations that we trapped and also had the coarsest gravel and rock underneath the ephemeral aeolian sand. At both these locations we captured several of the desert pocket mice (*Chaetodipus penicillatus*) and the Merriam's kangaroo rat (*Dipodomys merriami*).

We trapped Palm Springs pocket mice at each of 4 locations selected along a proposed habitat corridor (Mission Creek 1, 2, 3, and fault-line–power-line locations) linking the fault-line dunes–Willow Hole core reserve to the upper Mission Creek and Morongo Wash channels core reserve. At these locations, although we placed half of the traps within the active dry wash area and half on the more stabilized bank we only trapped Palm Springs pocket mice on the more stabilized benches and bank areas near the wash and not in the active wash channel. In the fault-line dunes were captured all Palm Springs pocket mice on the final night at the farthest location from the dunes, but still on the bank of dry wash drainage. This was also the case in Upper Thousand Palms Canyon, where we caught a Palm Springs pocket mouse just outside a dry wash drainage area, up on the bank where the soil was more compact and gravelly.

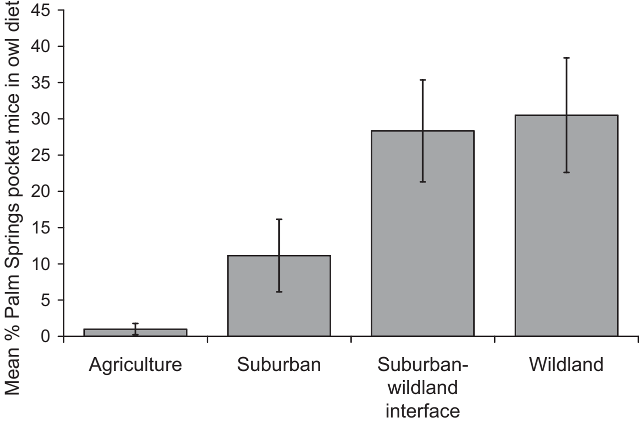

Figure 3. Results of burrowing owl diet analyses from summer 2009 partitioned by land use categories in the Coachella Valley. Bars indicate one standard error.

We collected and analyzed 560 burrowing owl pellets (1,443 prey items) with 65–225 pellets from each of 4 land-use categories (wildlands, suburban, wildland–suburban mix, and agriculture). Of these, we identified 340 Palm Springs pocket mice along with 135 individuals of other species of pocket mice, primarily the desert pocket mouse. Of those pellet collections that included Palm Springs pocket mice as prey, 90% (9/10) were within modeled suitable niche space with median HSI values $\geq$0.95, indicating correspondence between our model and locations where pocket mouse densities were sufficiently high to be regularly selected as prey by owls. Of those pellet collections that did not include Palm Springs pocket mice as prey, 80% were outside modeled suitable niche space with median HSI values $\geq$0.95. Comparing the occurrence of Palm Springs pocket mice in the owls' diet partitioned by surrounding land-use categories revealed significant differences (Fig. 3). Owl diets from landscapes dominated by agriculture and, high density suburban development, when combined had significantly fewer Palm springs pocket mice in their diet than the combined diets of those in wildland and wildland-suburban interface habitats (analysis of variance, d.f. $= 1$, $F = 4.14$, $P = 0.5$), indicating a potential negative relationship between more anthropocentric land-use types and pocket mouse occupancy.

DISCUSSION

Using historic location records we constructed niche models that identified the distribution of suitable habitat for the Palm Springs pocket mouse throughout the Coachella Valley. We then validated that model statistically using a random set of locations that were not employed in the model development, as well as using both live trapping and burrowing owl pellets. All methods were in concordance, indicating that our model was a robust representation of the potential distribution of this species. While there has been substantial loss of suitable habitat for Palm Springs pocket mice as a result of human land use changes, our model indicate large habitat areas remain, especially in the western portions of the valley. Conservation strategies to protect sustainable populations included habitat core areas and linkages between core areas (Dudek 2007). With our niche model we demonstrated that all identified core areas as well as most linkage corridors still included suitable Palm Springs pocket mouse habitat.

S. C. Dodd conducted extensive trapping for Palm Springs pocket mice within the Coachella Valley and the surrounding region, and found much higher densities in the northern and western Coachella Valley (unpublished report). These results, supported by our own trapping data, validate the patterns of suitable niche space indicated by our

ENM. S. C. Dodd did record positive Palm Springs pocket mouse captures at the 3 locations where we failed to detect them, but only after >1,000–2,000 trap nights, compared to the ≤80–240 trap nights we spent at any one location (S. C. Dodd, unpublished reports).

Other Coachella Valley floor species, such as the Coachella Valley fringe-toed lizard (*Uma inornata*) and flat-tailed horned lizard (*Phrynosoma mcallii*), have lost >90% of their historic suitable habitat (Barrows 2006; Barrows et al. 2008). In comparison, a much greater extent of suitable niche space for Palm Springs pocket mice remains undeveloped. Additionally, as Palm Springs pocket mouse habitat appears much less tied to retaining active aeolian and fluvial sand transport processes, the extent those processes have already been compromised should have less negative impact on the sustainability of Palm Springs pocket mouse populations than it has on the 2 lizards.

Our niche model, coupled with the results of others (S. C. Dodd, unpublished reports), indicates that Palm Springs pocket mice typically occur on alluvial fans with loose aeolian or alluvial sands often intermixed with coarser gravel. Palm Springs pocket mouse densities are highest in the relatively cooler mesic climate regime of the western and northern Coachella Valley. Our results indicate that the Palm Springs pocket mouse avoid the more dynamic active sand dunes that once occupied much of the center of the Coachella Valley and are less abundant on active ephemeral sand fields and dry washes. These patterns have implications to the potential effectiveness of corridors designated to ensure connectivity of protected Palm Springs pocket mouse populations.

Although our variable selection was limited by available GIS layers that covered the entire modeled area, those variables still provided important insights as to what constitutes suitable Palm Springs pocket mouse habitat. Soil conditions, specifically loose sandy soils have been noted by others in describing this species' habitat (Jameson and Peeters 1988; S. C. Dodd, unpublished report), and is consistent with the high sand and clay (as opposed to rock, just clay, or just sand) character of the variables included in our model. This plus the inclusion of vegetation type as a variable excluded the pure sand, active dunes that dominated the center of the Coachella Valley. The eigenvector weights for the ruggedness variables were low, meaning their contribution to the model was considerably less than the contribution of soil composition; nevertheless they focused the model on areas with gentle slopes. Although it needs further study, inclusion of ruggedness at 2 different scales may indicate that pocket mice prefer not only sites with gentle slopes at a scale corresponding to the mouse's home range, which would be expected, but also broader areas which could support a larger population base. Having a larger interacting population could reduce stochastic extinctions that can characterize smaller, isolated populations (Miller et al. 2009, Mitchell et al. 2010); the larger scale metric could then help identify suitable habitat for sustainable populations.

Based on our ENM, remaining habitat for the Palm Springs pocket mouse in the southeastern Coachella Valley consists of patches of various sizes, with much of the historic levels of connectivity lost largely due to agricultural land conversion. Contiguous habitat in the northern and western portions of the Coachella Valley indicates that historically this area would have likely supported one large and unfragmented Palm Springs pocket mouse population. More recent anthropogenic road development and urbanization have fragmented this landscape and increased threats from stray dogs and cats and compaction of sandy soils from off-road vehicle (ORV) use (CVAG 2006). The extent to which roadways create barriers to small mammal movements has been examined in other species, but not the Palm Springs pocket mouse. Those studies have shown that some road types constitute significant but not impermeable barriers to those species (Clark et al. 2001, McGregor et al. 2008). Pocket mice may be reticent to cross roads because they lack the loose sand and shrub cover mice appear to prefer; such reticence may be due to an increase in predation risks on those roads or due to other factors (Jameson and Peeters 1988; S. C. Dodd, unpublished report). We designed our analyses to identify the distribution and relative suitability of habitat along potential corridors; we did not examine the effect of barriers such as roadways on the effectiveness of those corridors to provide connectivity for Palm Springs pocket mouse. Permeability of these barriers should be a priority study of the impacts of development on this and other corridor dwelling species.

MANAGEMENT IMPLICATIONS

Connectivity is a widely accepted characteristic of sound conservation design, yet corridor characteristics, especially habitat composition within those corridors have received insufficient attention in most designs to date. Linkages for corridor dwellers must include habitat for sustaining multigenerational populations. This requires evaluating whether continuous suitable habitat exists within proposed corridors. Our research demonstrates how niche modeling can provide a landscape-scale view of the distribution of suitable habitat to evaluate conservation objectives for connectivity. Through niche modeling and live trapping we identified suitable corridor characteristics, including soil, vegetation, and topographic characteristics as well as the impact of disturbance regimes. These findings can then be directly translated into specific design and management considerations as the conservation plan is implemented.

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Using ecosystem integrity to maximize climate mitigation and minimize risk in international forest policy

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Several key international policy frameworks involve forests, including the Paris Agreement on Climate Change and the Convention on Biological Diversity (CBD). However, rules and guidelines that treat forest types equally regardless of their ecosystem integrity and risk profiles in terms of forest and carbon loss limit policy effectiveness and can facilitate forest degradation. Here we assess the potential for using a framework of ecosystem integrity to guide policy goals. We review the theory and present a conceptual framework, compare elements of integrity between primary and human-modified forests, and discuss the policy and management implications. We find that primary forests consistently have higher levels of ecosystem integrity and lower risk profiles than human-modified forests. This underscores the need to protect primary forests, develop consistent large-scale data products to identify high-integrity forests, and operationalize a framework of ecosystem integrity. Doing so will optimize long-term carbon storage and the provision of other ecosystem services, and can help guide evolving forest policy at the nexus of the biodiversity and climate crises.

KEYWORDS

Paris Agreement, primary forest, carbon, forest degradation, deforestation

Introduction

Forest ecosystems are central to international agreements and frameworks that support and set policy agendas, including the United Nations (UN) Framework Convention on Climate Change (UNFCCC), Convention on Biological Diversity (CBD), Sustainable Development Goals (SDGs), and Convention to Combat Desertification (UNCCD). Forests and their ecosystem services provide critical data to inform global environmental assessments such as the Global Forest Resource Assessments (FRAs) of the UN Food and Agriculture Organization (FAO), the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), the System of Environmental Economic Accounting–Ecosystem Accounting (SEEA-EA), and the World Bank's reports on the Changing Wealth of Nations (Lange et al., 2018). The mitigation significance of forests is recognized in Article 5 of the Paris Agreement. Given their mitigation value, updating forest management practices to reduce emissions and increase withdrawals from the atmosphere should be included in many countries' Nationally Determined Contributions (NDCs; Forsell et al., 2016; Grassi et al., 2017; Roe et al., 2019). Forestry practices have the potential to provide a majority fraction of the Agriculture, Forestry, and Other Land Use (AFOLU) sector's contributions to climate mitigation, which may represent up to one-third of net emission reductions needed to limit warming below 1.5–2°C above pre-industrial levels (Federici et al., 2017; Grassi et al., 2017; Griscom et al., 2017; Roe et al., 2019). The current emissions gap between NDCs and what is required to limit warming to 1.5 or 2°C (UNEP, 2019) means that the role of forests may be even greater; for example, forests are referenced heavily in the Intergovernmental Panel on Climate Change (IPCC) special report on 1.5°C in the context of negative emissions (Dooley et al., 2018; IPCC, 2018).

However, given the finite area of available land and the many ecosystem services they provide, there are often conflicting goals for the management of forests in national and international policy contexts, resulting in incoherent policies and policy objectives (Kalaba et al., 2014; Koff et al., 2016; Tegegne et al., 2018; Timko et al., 2018). For example, many of the UN SDGs focused on promoting economic development are at odds with conserving forests and biodiversity (Ibisch et al., 2016). Unclear and inconsistent definitions and accounting rules mean that forest mitigation measures can have a range of results from large-scale protection that preserves carbon storage, sequestration, and ecosystem services, to perverse outcomes with net carbon loss, degraded ecosystems, and negative impacts on other policy goals (Mackey et al., 2013). For example, bioenergy with carbon capture and storage (BECCS) is used in the majority of current global socioeconomic model scenarios to stay below 1.5–2°C of warming (Roe et al., 2019). At these scales, BECCS will require the conversion of vast quantities of native forests into tree plantations or short-rotation forests (Fuss et al., 2014; Creutzig et al., 2015; Smith et al., 2016; IPCC, 2018). Increased bioenergy use is currently resulting in forest degradation and deforestation that will generate net carbon emissions for decades or longer (Birdsey et al., 2018; Booth, 2018; Sterman et al., 2022). Part of the problem is that forest cover and types are largely seen as fungible within the UNFCCC guidelines (UNFCCC, 2002), with no criteria for forest condition or carbon longevity (Ajani et al., 2013; Hansen A. J. et al., 2020; Keith et al., 2021).

From a carbon perspective, "risk of loss" of the stock is of central importance. The risk of loss from disturbances means that some land-based carbon activities will not provide long-term protection of carbon from release into the atmosphere (e.g., Anderegg et al., 2020). This risk is a primary reason that forest-based solutions are often not considered as reliable ways to reduce net emissions and hence are not prioritized as mitigation activities (Grassi et al., 2017). Yet little consideration has been given to differentiating forest types and management schemes based on their "risk of loss" profiles. The Paris Agreement mentions criteria for mitigation that speak to risk, such as equity, sustainability, and integrity, but as of yet there is little guidance on implementation.

The concept of "ecosystem integrity," or related "ecological integrity," has a long history in theoretical and applied ecology (e.g., Kay, 1991; Tierney et al., 2009; Wurtzebach and Schultz, 2016) and is explicitly referenced [e.g., Paris Agreement, CBD post-2020 Global Biodiversity Framework (Convention on Biological Diversity [CBD], 2021), IPCC Working Group II (IPCC, 2022)] or implied in international agreements and national-level legislation and agency directives (e.g., Australian Government, 1999). By providing a holistic view of ecosystem structure, function, composition, and adaptive capacity, the objective of maximizing ecosystem integrity may have the potential to minimize risk of carbon loss and maximize the ecosystem services provided by forests, thereby facilitating greater policy coherence across sectors (Koff et al., 2016; Dooley et al., 2018; Barber et al., 2020). However, the concept is not prioritized in international policy nor operationalized in most national forest policies, thus falling well short of its potential. There are no specific actions or supporting mechanisms for ecosystem integrity in the Paris Agreement, and parties have not articulated how they will identify and protect high-integrity ecosystems. Instead of representing a guiding framework, ecosystem integrity is largely viewed as a potential co-benefit (Bryan et al., 2016; Funk et al., 2019). Particularly important is providing a definition and framework for ecosystem integrity that the CBD (though the Global Biodiversity Framework) and the UNFCCC (through the Global Stocktake) can utilize to achieve their biodiversity and climate mitigation objectives.

Here we review the potential for a framework of ecosystem integrity to minimize risk in forest-based mitigation policies and maximize ecosystem service co-benefits. We first discuss the theory of ecosystem integrity and provide a working conceptual framework. We then compare important elements of ecosystem integrity between primary and human-modified forests, with a focus on elements most relevant for carbon mitigation including risk profiles. Finally, we discuss the policy and management implications of this comparative analysis. By drawing on ecological theory and several sub-disciplines within ecology, we integrate knowledge into a coherent framework of ecosystem integrity (**Figure 1**) that can be used to guide both forest policy at the international level as well as implementation in the form of land use decisions, metrics, and priorities at the national and jurisdictional levels. Our review draws upon decades of evolving forest policy and published literature, including but not limited to peer-reviewed articles, as well as engagement with stakeholders, practitioners, policy makers, and forest ecologists.

Framework for forest ecosystem integrity

Definition

Many definitions of ecosystem integrity exist because ecosystem integrity is not a simple absolute physical property but rather a multidimensional and scale-dependent emergent phenomenon that encompasses important system components and their interactions. The concept has received considerable attention over the past several decades because of the human benefits derived from natural processes and ecosystem states. As noted by Muller et al. (2000), “ecosystem integrity turns out to be the ecological branch of sustainability.”

Here we adopt and build upon the general framework originally provided by Kay (1991), whereby ecosystem integrity *integrates different characteristics of an ecosystem that collectively describe its ability to achieve and maintain its optimum operating state, given the prevailing environmental drivers and perturbations, and continue its processes of self-organization and regeneration (i.e., autopoiesis)*. One of the main theoretical divides about ecosystem integrity relates to differentiating compositional (e.g., species richness, genetic diversity, or presence of threatened species), structural (e.g., vegetation density, biomass, food chains, and trophic levels) or functional (e.g., productivity, energy flows, and nutrient cycling) aspects of integrity (De Leo and Levin, 1997; Pimentel et al., 2013; Roche and Campagne, 2017). We suggest these are largely inseparable given the fundamental importance of structural and compositional elements in supporting functional forest ecosystem integrity and the many interdependencies among composition, structure, and function. In practice, available data and resources will determine what can be measured at a particular spatial and temporal scale. Because ecosystem integrity includes the provision of ecosystem services for human benefit, its evaluation typically includes a human dimension (Kay, 1991; De Leo and Levin, 1997; Kay and Regier, 2000; Dorren et al., 2004; Roche and Campagne, 2017).

Components of ecosystem integrity

Based on decades of theoretical and applied studies, we provide a framework for understanding the components of forest ecosystem integrity, their drivers, and their inter-linkages (**Figure 1**). It is important to note that all elements of ecosystem integrity are affected by the prevailing environmental and site characteristics of a given forested location, which must be accounted for when comparing specific locations in space and/or time.

Foundational elements

Forest ecosystem integrity is based on physiological structures that efficiently use and dissipate energy (**Figure 1**). These dissipative structures, or “ecological orientors” (Muller et al., 2000), generate a gradient of energy degradation *via* metabolic reactions that create and maintain themselves (i.e., self-organization). Progressively accumulated exergy (i.e., available energy) becomes stored emergy (i.e., all the energy used to generate a product or service) (Campbell, 2000; Kay and Regier, 2000; Muller et al., 2000). Over the course of evolution, community assembly, and forest succession, this process generates optimized (generally high but not too high; Hengeveld, 1989; May, 2001) ecosystem complexity and distance from thermodynamic equilibrium (Odum, 1969; Kay, 1991; Holling, 1992; Campbell, 2000; Muller et al., 2000), with associated levels of structural complexity, functional diversity, and niche complementarity (Tilman, 1996; Tilman and Lehman, 2001; Thompson et al., 2009). Ecosystem processes that sustain and regulate this self-organizing system, such as productivity, evapotranspiration, reproduction cycles, and nutrient cycling and retention, are optimized in the process (Muller et al., 2000; Dorren et al., 2004; Migliavacca et al., 2021). The resulting forest is a non-linear, self-organizing, holarchic and open system, with reciprocal power relationships between levels (Kay and Regier, 2000).

A critical property of ecosystem integrity that is difficult to assess from structural or compositional elements alone is stability. Following Grimm and Wissel (1997), stability is comprised of resistance (or constancy), resilience, and persistence, which collectively represent an ecosystem’s ability to resist or be resilient to change at both short and long time scales (Kay, 1991, 1993; Regier, 1993; Muller, 1998; Kay and Regier, 2000; Andreasen et al., 2001; Parrish et al., 2003). In the case of forest ecosystem integrity, primary drivers of change (exposure) include human land use and other human pressures, and climate change including extreme weather events and increasing disturbances. Resistance indicates a forest’s ability to maintain stability *via* dynamic equilibrium within defined ecosystem

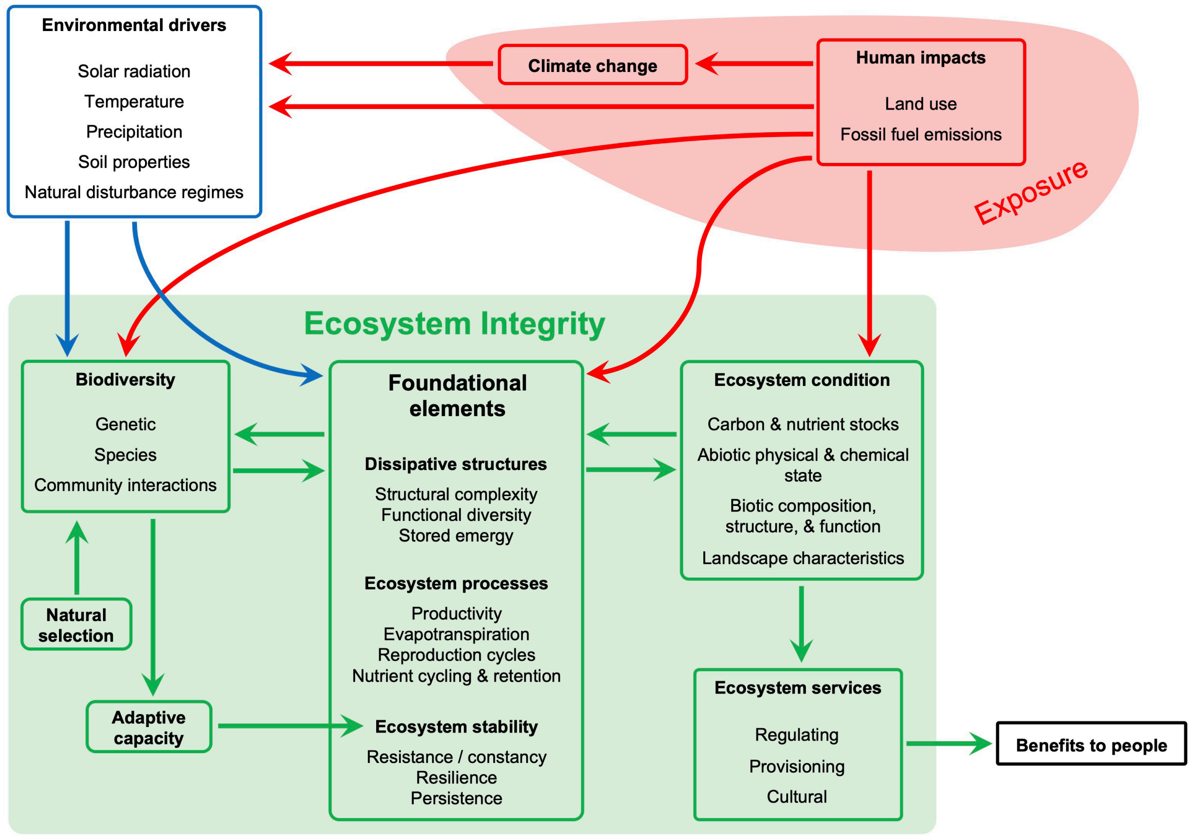

FIGURE 1
Conceptual framework of ecosystem integrity. Integrity is based on foundational elements including dissipative structures, ecosystem processes, and ecosystem stability. These are underpinned by biodiversity, natural selection, and adaptive capacity, and in turn generate a given ecosystem condition and benefits to people. Ecosystem integrity is impacted by environmental drivers and human impacts, including land use and climate change.

bounds (Hughes et al., 2002; Loreau et al., 2002) in response to these drivers. Forest resistance is conferred by negative feedbacks and buffers, for example stable microhabitats in forest interiors and functional redundancy across species. Resilience indicates the ability to return to optimal operating conditions after a state-altering perturbation (Holling, 1973; Kay, 1991; Kay and Regier, 2000; Muller et al., 2000; Thompson et al., 2009). The resulting ecosystem state can be somewhat altered (i.e., "ecological resilience" as opposed to "engineering resilience"), but when viewed over an appropriate time span, a resilient forest is able to maintain its "identity" in terms of taxonomic composition, structure, ecological functions, and process rates–and hence exhibit persistence (Thompson et al., 2009). Forest resilience is generally conferred by regenerative capacity *via* biological legacies (Franklin et al., 2000; Lindenmayer et al., 2019). These components of stability are supported by an ecosystem's adaptive capacity, or the capacity for adaptive change in response to new conditions (Angeler et al., 2019). For example, genetic diversity, species diversity, and phenotypic plasticity allow for varied and time-evolving expression of adaptive traits and species within an ecosystem in response to changing environmental conditions, disturbances, or other pressures (Savolainen et al., 2007; Reed et al., 2011; Rogers et al., 2017). Hence, adaptive capacity is supported by biodiversity (**Figure 1**).

Biodiversity

These foundational elements of integrity are derivatives of the underlying biodiversity of a forest ecosystem, including diversity at the genetic, species, and community levels (**Figure 1**). A wealth of literature provides evidence that biodiversity supports net primary productivity (Chapin et al., 1997; Diaz and Cabido, 2001; Hooper et al., 2005; Thompson et al., 2009; Tilman et al., 2014; Liang et al., 2016; Duffy et al., 2017; de Souza et al., 2019; Matos et al., 2020), adaptation (Steffen et al., 2015; King et al., 2019), resistance (Pimm, 1984; Walker, 1995; Ives et al., 1999; Lehman and Tilman, 2000; McCann, 2000; Loreau et al., 2002; Dorren et al., 2004; Hooper et al., 2005; Thompson et al., 2009; Hautier et al., 2015), resilience (Peterson et al., 1998; Loreau et al., 2001;

Hooper et al., 2005; Drever et al., 2006; Thompson et al., 2009; Ajani et al., 2013; Oliver et al., 2015; King et al., 2019), functional diversity (Cadotte et al., 2011; Levin, 2013; Karadimou et al., 2016), and overall ecosystem functioning (e.g., Lawton, 1997; Tilman, 1997; Hooper et al., 2005; Cardinale et al., 2012; Watson et al., 2018; King et al., 2019). These relationships exist because natural selection yields the characteristic biodiversity and phenotypic plasticity best suited to prevailing environmental conditions, including fluctuating resource inputs, extreme events, periods of stress, and natural disturbances. Specific mechanisms include biotic control of grazing, population density, and nutrient cycling; niche selection and complementarity; biotic and abiotic facilitation; and functional redundancy (i.e., the "insurance hypothesis") (e.g., Naeem et al., 1995; Tilman, 1996; Tilman et al., 1997; Yachi and Loreau, 1999; Loreau, 2000; Tilman and Lehman, 2001; Pretzsch, 2005; Scherer-Lorenzen and Schulze, 2005; Jactel and Brockerhoff, 2007; Thompson et al., 2009; Hantsch et al., 2014; Wright et al., 2017; Liu et al., 2018).

Ecosystem condition

The foundational elements of ecosystem integrity form the basis for assessing ecosystem condition (Keith et al., 2020), specifically in the context of the System of Environmental-Economic Accounting (Committee of Experts on Environmental-Economic Accounting, 2021). Ecosystem condition is defined as "the quality of an ecosystem that may reflect multiple values, measured in terms of its abiotic and biotic characteristics across a range of temporal and spatial scales" (Keith et al., 2020). Ecosystem condition is measured in terms of variables that reflect the state, processes, and changes in the ecosystem, including (i) carbon and nutrient stocks, (ii) abiotic physical and chemical states such as water quantity and quality; (iii) biotic composition, structure, and function; and (iv) landscape diversity and connectivity. Indicators of condition are derived when variables are transformed by assessment against a reference condition. For a given biome and prevailing environmental conditions, these state variables are optimized by the foundational elements of ecosystem integrity and biodiversity (Phillips et al., 1994; Thompson et al., 2009; Roche and Campagne, 2017; Di Marco et al., 2018; Liu et al., 2018).

Ecosystem services

Characteristics of ecosystem condition that relate to the supply of ecosystem services represent an instrumental anthropocentric dimension. Specific ecosystem services can be linked to characteristics of ecosystem condition, and condition indicators can be associated with multiple services (Keith et al., 2020). Ecosystem services can be broadly categorized as regulating, provisioning, and cultural services (Millennium Ecosystem Assessment, 2005; Kandziora et al., 2013; IPBES, 2019; Committee of Experts on Environmental-Economic Accounting, 2021). Regulating services include clean and regulated water flow, air quality, pest and pathogen containment, erosion control, nutrient regulation, resistance and resilience to natural hazards, waste regulation, carbon sequestration and storage, and climate regulation from local to global scales. Provisioning services include the animals, plants, and minerals used for food, medicine, energy, and infrastructure. Cultural services include customary values, ecotourism and nature-based recreation, scientific research, and education.

The concept of ecosystem integrity is useful because it integrates across many properties of forest ecosystems, and thereby optimizes values useful to humans and other organisms. In the words of Koff et al. (2016), "ecosystem integrity is a scientific paradigm that fits the political needs of the present global development agenda focused on complex human-environmental interactions." The concept is holistic and can be adapted to local, national, or international contexts. At jurisdictional levels, the related concepts of "ecological integrity" and "biological integrity" have been used operationally to provide benchmarks for natural resource management (Karr, 1996; Harwell et al., 1999; Campbell, 2000; Muller et al., 2000; Parrish et al., 2003; Tierney et al., 2009; Wurtzebach and Schultz, 2016; Roche and Campagne, 2017). However, as noted above, the international policy community has yet to implement these terms. This is important because ecosystem integrity may be directly linked to forest and carbon risk profiles that, if understood and prioritized, could greatly aid our ability to utilize forests for mitigation and adaptation.

Comparison of ecosystem integrity between forest types

Here, we compare components of ecosystem integrity most relevant for international policy across commonly recognized broad categories of forest types, focusing on primary forests and forests with significant levels of human modification and pressure. We focus on components of ecosystem integrity most pertinent to forest-based climate mitigation, including forest risk profiles as governed by exposure and stability as well as carbon stocks and fluxes. As noted previously, direct comparisons between forest types must account for environmental and site drivers, including the prevailing biome (e.g., tropical, temperate, or boreal) and heterogeneity within as determined by climate, soils, hydrology, and natural disturbance regimes.

Following Kormos et al. (2018), Food and Agriculture Organization of the United Nations [FAO] (2020), and IUCN (2020), primary forests are defined as: (i) largely undisturbed by industrial-scale land uses such as logging, mining, hydroelectric development, and road construction; (ii) established and regenerated by natural biological, ecological, and evolutionary processes; (iii) including the full range of successional stages at a landscape level from pioneer, secondary growth, and old-growth forest stands; and (iv) with the vegetation structure, community networks, and taxonomic composition principally reflecting natural processes including natural disturbance regimes. Primary forests can therefore be distinguished from naturally regenerating forests that are subject to conventional forestry management for commodity production (Puettmann et al., 2015), as well as planted forests, including plantations. For our purposes, primary forest therefore encompasses a range of commonly recognized forest descriptors including intact, virgin, ecologically mature, and old growth forests (Buchwald, 2005; Mackey et al., 2013; DellaSala et al., 2022b).

Foundational elements of ecosystem integrity

Comparison of dissipative structures

In this section we focus on structural complexity because of its importance for carbon stocks. Other components of dissipative structures (**Figure 1**) will be highlighted for their role in supporting ecosystem integrity in following sections (including functional diversity as it relates to biodiversity in the section "Biodiversity," and stored emergy as manifested in biomass and carbon stocks in section "Ecosystem condition"). High-integrity forests that have been allowed time to respond to their emergy signature develop a set of relatively complex ecosystem structures (Campbell, 2000). Canopy structure is particularly influential for other elements of ecosystem integrity such as microclimate, runoff, nutrient cycling, and biodiversity (Hobbie, 1992; Parker, 1995; Didham and Lawton, 1999; Siitonen, 2001; Asner et al., 2010; Goetz et al., 2010; Hansen et al., 2014). Primary tropical forests in particular develop tall, multi-story dense canopies with large variations in plant size and emergent canopy dominants (Kricher, 2011; Hansen A. J. et al., 2020). Temperate forests also develop complex forest canopies as they age, which is associated with high levels of biodiversity and carbon storage (DellaSala et al., 2022b).

Canopy height, in turn, is positively related to aboveground biomass and carbon storage. For example, in Brazil, Democratic Republic of the Congo, and Indonesia, primary forests were 38–59% taller and contained 70–148% more aboveground biomass than other dense tree cover types, including degraded forests, secondary regrowth, and tree plantations (Turubanova et al., 2018). When felling the largest trees or clear-cutting entire stands, logging decreases canopy height, homogenizes forest canopies, and reduces structural complexity (Pfeifer et al., 2016; Rappaport et al., 2018; Bourgoin et al., 2020), which can take centuries to recover. Structural complexity also relates to non-living forest structures, such as dead wood, that provide supporting functions including nutrient cycling, soil formation, and habitat for myriad species (Janisch and Harmon, 2002; Millennium Ecosystem Assessment, 2005; Gamfeldt et al., 2013). When directly compared, primary forests consistently contain a greater volume and diversity of dead wood than forests managed for commodity production (e.g., Guby and Dobbertin, 1996; Siitonen et al., 2000; Siitonen, 2001; Debeljak, 2006).

Comparison of ecosystem processes

Here we focus on ecosystem productivity given its importance for climate mitigation, but note that other ecosystem processes will be highlighted in following sections (evapotranspiration as it relates to drought risk in section "Comparison of risks from drought," reproduction cycles as they relate to regeneration in section "Comparison of regenerative capacity," and nutrient cycling and retention as it relates to nutrient stocks in section "Comparison of ecosystem condition"). Differences in ecosystem productivity and carbon fluxes among forest seral stages have been the subject of much debate. One viewpoint is that forests containing younger trees are more productive, with both higher net primary productivity (NPP, including photosynthesis and autotrophic respiration) and net ecosystem productivity (NEP, also including heterotrophic respiration) than ecologically mature forests (e.g., Ryan et al., 1997; Simard et al., 2007; Goulden et al., 2010). This view has often justified the conversion of primary forests into regrowth forests. While it is true that secondary forests often have higher rates of photosynthesis, this is not always the case, particularly when accounting for the impacts of higher species richness in older primary forests (Liu et al., 2018) and the entire age profile of timber rotations, including times with bare soil and young trees. A wealth of evidence clearly shows that old-growth forests continue to sequester carbon in significant quantities in aboveground biomass, dead wood, litter, and soil organic matter (Phillips et al., 1998; Zhao and Zhou, 2006; Luyssaert et al., 2008; Lewis et al., 2009; Thompson et al., 2013; Gatti et al., 2014; Grace et al., 2014; McGarvey et al., 2015; Schimel et al., 2015; Lacroix et al., 2016; Baccini et al., 2017; Phillips and Brienen, 2017; Qie et al., 2017; Lafleur et al., 2018; Mitchard, 2018). This is why Pugh et al. (2019) found that old-growth forests (defined in that study as > 140 years) cover roughly 39% of global forest area and contribute 40% of the current global forest carbon sink, which in turn represents roughly two-thirds of the terrestrial carbon sink (Friedlingstein et al., 2019).

More importantly, when comparing these CO_2 fluxes in the context of mitigation actions, the entire life cycle of management and disturbance must be taken into account. From a carbon balance perspective, converting primary forests into young forests logged for biomass energy, wood supply, or other uses does not offset the original conversion emissions for many decades to centuries (Cherubini et al., 2011; Holtsmark, 2012; Mitchell et al., 2012; Keith et al., 2015; Birdsey et al., 2018; Hudiburg et al., 2019; Malcolm et al., 2020), creating a large carbon debt on policy-relevant timescales (generally years to 1–3 decades). Hence the size, longevity, and stability of accumulated forest carbon stocks, including in the soils, are important mitigation metrics in addition to the rate of annual sequestration (Mackey et al., 2013; Keith et al., 2021).

Stability and risk profiles

Ecosystem stability is comprised of resistance, resilience, and longer-term persistence (**Figure 1**). Combined with exposure to external perturbations, properties of ecosystem stability provide critical information for risk assessments. Risk assessments are undertaken and utilized in a wide variety of scientific and operational contexts (Fussel and Klein, 2006; Glick et al., 2011; Oppenheimer et al., 2014; Rogers et al., 2017), and are critically important to ensure mitigation actions result in long-term carbon storage. Nevertheless, risk assessments are currently either not undertaken or done so in mostly rudimentary and incomplete ways for forest-based carbon mitigation (Mignone et al., 2009; Ajani et al., 2013; Anderegg et al., 2020). Here we focus on the risk of a forest ecosystem experiencing a state-altering disturbance that results in carbon loss to the atmosphere.

Comparison of risks from wildfire

Wildfires are major natural disturbances in temperate and boreal forest ecosystems, although historically rare in tropical wet forests unless caused by humans (Randerson et al., 2012; Archibald et al., 2013; Giglio et al., 2013; Andela et al., 2017). The area burned by wildfire has been increasing in high-canopy cover forests globally over the past 20 years (Andela et al., 2017), and human-caused fires are a major driver of the loss of intact forest landscapes (Potapov et al., 2017). Extreme fire weather conditions have increased in most forests globally over the last half-century (Jolly et al., 2015; Jain et al., 2017; Dowdy, 2018), and wildfires are projected to become more widespread and intense due to climate change (Ward et al., 2012; Flannigan et al., 2013; Abatzoglou et al., 2019; Dowdy et al., 2019; Rogers et al., 2020). Humans have increased forest fire risk by augmenting forest fuels through active management (DellaSala et al., 2022a) and by increasing the number and sources of ignition (Balch et al., 2017). The majority of documented megafires globally have been started by humans under extreme fire weather conditions (Ferreira-Leite et al., 2015; Bowman et al., 2017).

A large body of literature shows that forests managed for commodity production, degraded, or disturbed forests are generally more susceptible to fires because of drier microclimates and fuels, higher land surface temperatures that promote air movement between forests and neighboring open areas, and human ignitions due to access and proximity, particularly in the tropics (e.g., Uhl and Kauffman, 1990; Holdsworth and Uhl, 1997; Cochrane et al., 1999; Laurance and Williamson, 2001; Siegert et al., 2001; Donato et al., 2006; Lindenmayer et al., 2009, 2011; Brando et al., 2014; DellaSala et al., 2022a). Although fires are a natural disturbance agent throughout most boreal forests (Viereck, 1973; Payette, 1992; Gromtsev, 2002; Soja et al., 2007; Rogers et al., 2015), fire frequency in boreal forests increases in proximity to human land use due to fuel drying, human access, and forestry practices such as leaving slash on site, particularly in Siberia (Kovacs et al., 2004; Achard et al., 2008; Ponomarev, 2008; Laflamme, 2020; Terrail et al., 2020; Shvetsov et al., 2021).

In many forest systems, fires in previously logged or managed landscapes can be more intense/severe, emit more carbon to the atmosphere, and take longer to recover than fires in ecologically mature or primary forests due to increased fuel availability, lower fuel moisture, and dense secondary forests that carry crown fires and are susceptible to extensive tree mortality (Odion et al., 2004; Stone et al., 2004; Thompson et al., 2007; Lindenmayer et al., 2009, 2011; Price and Bradstock, 2012; Kukavskaya et al., 2013; Taylor et al., 2014; Bradley et al., 2016; Dieleman et al., 2020; De Faria et al., 2021; Landi et al., 2021). In general, larger and older trees have a greater chance of surviving fires due to thicker bark and lower relative scorch height (Laurance and Williamson, 2001; Lindenmayer et al., 2019). Increased fuel availability in secondary forests can also facilitate fire spread (Lindenmayer et al., 2011). Positive feedbacks between fires and secondary vegetation can lead to permanent forest loss, i.e. "landscape traps," at the warm / dry edge of forest ranges (Payette and Delwaide, 2003; Hirota et al., 2011; Lindenmayer et al., 2011; Staver et al., 2011; Brando et al., 2014; Kukavskaya et al., 2016; Lindenmayer and Sato, 2018). Primary forests are generally more resistant to fire because of higher humidity and fuel moisture, the presence of understory species such as ferns and mosses that limit light penetration to the forest floor and increase water retention, and much less human access (Ough, 2001; Lindenmayer et al., 2009; Taylor et al., 2014; Zylstra, 2018; Funk et al., 2019).

Comparison of risks from drought

Severe droughts represent 60–90% of climate extremes impacting gross primary productivity in the past 30 years (Zscheischler et al., 2014), are a major driver of tree mortality and forest die-off (Allen et al., 2010, 2015; Anderegg et al., 2013; McDowell and Allen, 2015; McDowell et al., 2016; Rogers et al., 2018), and are expected to increase with future climate change (Cook et al., 2014; Trenberth et al., 2014; Yi et al., 2014; Xu et al., 2019; Zhou et al., 2019; De Faria et al., 2021). A large body of literature indicates closed canopy forests are more resistant to drought, particularly in the tropics, due to shading, biophysical microclimate buffering, thicker litter layers, deeper roots, and increased water use efficiency as trees develop (e.g., Briant et al., 2010; von Arx et al., 2013; Frey et al., 2016; Brienen et al., 2017; Qie et al., 2017; Giardina et al., 2018; Caioni et al., 2020; Elias et al., 2020). For a given level of realized drought, some evidence points to larger older trees being more susceptible to drought impacts (Phillips et al., 2010; Girardin et al., 2012; Bennett et al., 2015; McDowell and Allen, 2015; McIntyre et al., 2015; Chen et al., 2016; Clark et al., 2016). Yet there is also contrasting evidence. For example, younger boreal forests can be more susceptible to drought compared to mature forests (Luo and Chen, 2013; Hember et al., 2017) due to competition for space and nutrients and less extensive and shallower root systems. Tree diversity, which is generally higher in primary compared to human-modified forests (see section "Biodiversity"), may increase resistance and resilience to drought *via* adaptive responses and functional redundancy (Jump et al., 2009; Sthultz et al., 2009; Dale et al., 2010; Harter et al., 2015), and intact forest canopies can be relatively resistant and resilient to short-term climate anomalies including drought (Williamson et al., 2000; Saleska et al., 2007). Evidence also suggests that mechanical "thinning," which is frequently proposed and implemented to combat drought, decreases stand-level water use in the short-term but actually increases individual tree water demand *via* higher leaf-to-sapwood ratios and hence drought vulnerability in the long-term (McDowell et al., 2006; Kolb et al., 2007; D'Amato et al., 2013; Clark et al., 2016).

Mature forests transpire large quantities of water from relatively deep in the soil profile, increasing regional cloud cover and precipitation. This acts to increase the proportion of "recycled" water within a given region and thereby decreases the prevalence of regional droughts (Foley et al., 2007; Spracklen et al., 2012; Ellison et al., 2017). For example, air passing over intact tropical forest landscapes can contain twice the moisture content as air over degraded forests or non-forest landscapes (Sheil and Murdiyarso, 2009). Degradation and the loss of intact forest landscapes increases dry and hot days, decreases daily rainfall intensity and levels, and exacerbates regional droughts (Deo et al., 2009; Alkama and Cescatti, 2016).

Comparison of risks from pests and pathogens

Pests and pathogens are an increasing threat to many forests globally, particularly as climate change alters life cycles, potential ranges, and host-pest interactions (Carnicer et al., 2011; Kautz et al., 2017; Seidl et al., 2017; Simler-Williamson et al., 2019). Mature boreal and temperate forests can be more susceptible to pests and pathogens compared to younger forests, in part due to decreases in the resin flow of defense compounds (Christiansen and Horntvedt, 1983; Hansen and Goheen, 2000; Baier et al., 2002; Dymond et al., 2010). Prominent examples include bark beetle and defoliator susceptibility (Kurz et al., 2008; Raffa et al., 2008; Taylor and MacLean, 2009; Krivets et al., 2015; Kautz et al., 2017). Nevertheless, ecologically mature forests tend to be resilient to biotic infestations, as these cyclical events initiate succession and lead to stand- and landscape-level heterogeneity (Holsten et al., 2008; Thompson et al., 2009). Moreover, tree diversity (measured in terms of genetic, species, and age) tends to limit pest and pathogen spread and damage because of resource dilution, host concealment, phenological mismatches, increased predators and parasitoids, alternative hosts, and metapopulation dynamics (Root, 1973; Karieva, 1983; Pimm, 1991; Watt, 1992; Zhang et al., 2001; Jactel et al., 2005; Pautasso et al., 2005; Scherer-Lorenzen and Schulze, 2005; Thompson et al., 2009; Guyot et al., 2016).

In terms of human influence, anthropogenic disturbances such as selective logging can introduce forest pests and diseases (Gilbert and Hubbell, 1996), including non-native, and evidence suggests forest edges and logged forests are more susceptible to beetle attacks due to increases in available host niches and altered moisture conditions (Sakai et al., 2001). Many pests, particularly in temperate and boreal forests, take advantage of weakened tree defenses during drought (Raffa et al., 2008; McDowell et al., 2011; Anderegg and Callaway, 2012; Hicke et al., 2012; Keith et al., 2012; Poyatos et al., 2013; Anderegg et al., 2015). Monocultures, or tree plantations, have been shown to be particularly vulnerable due to a lack of tree diversity, high tree density, and the associated host-pest interactions (Jactel et al., 2005; Macpherson et al., 2017; Lee, 2018).

Comparison of risks from windthrow

Windthrow events can lead to forest mortality and are expected to increase in some regions with climate change (Klaus et al., 2011; Saad et al., 2017). Although these events are somewhat stochastic, they are also influenced by soils, orography, regional climate regimes, and forest composition and structure. Similar to the risks of pests and pathogens, within a given stand there is evidence that older and taller trees are more susceptible to windthrow due to the physics of taller trees and root rot (Lohmander and Helles, 1987; Ruel, 1995). Nevertheless, fragmented or thinned forests experience elevated mortality and collapse of trees from windthrow because of increased exposure (Laurance and Curran, 2008; Reinhardt et al., 2008; Schwartz et al., 2017).

Comparison of risks from species range shifts

Climate regimes have strong influences on the potential and realized ranges of forest tree species, evidenced by the paleoecological record (Overpeck et al., 1991; DeHayes et al., 2000; Davis and Shaw, 2001) and current assemblages (e.g., Neilson, 1995; Foley et al., 2000), and considerable scientific effort is focused on projecting future responses to climate change (e.g., Sitch et al., 2003; Elith and Leathwick, 2009; Rogers et al., 2011, 2017; Ehrlen and Morris, 2015; Prasad et al., 2020). How trees and forest ecosystems will respond is uncertain due to complex interactions between the pace of climate change, physiological tolerances, dispersal and migration rates, phenotypic plasticity and adaptation, the presence of climate refugia, migration of associated species / symbionts, and forest fragmentation, among others (Davis and Shaw, 2001; Iverson et al., 2004; Jump and Penuelas, 2005; Mackey et al., 2008; Nicotra et al., 2010; Prasad, 2015; Rogers et al., 2017). In general, current and projected climate change is expected to degrade biodiversity due to species extinctions and the contraction of realized ranges (Miles et al., 2004; Campbell et al., 2009). Forest and landscape fragmentation in particular is known to hinder resilience and species migration because of the loss of suitable areas for dispersal and limitations on gene flow (Collingham and Huntley, 2000; Loreau et al., 2002; Scheller and Mladenoff, 2008; Thompson et al., 2009). Large areas of primary forests are expected to have higher adaptive capacity and stability compared to forests under human pressure because of their connectivity, biodiversity, and microclimate buffering (Mackey et al., 2015; Watson et al., 2018; Thom et al., 2019; see section "Biodiversity").

Comparison of risks from land use degradation

Human land use pressures on forests generally result in both direct environmental impacts as well as further, often unplanned, degradation or deforestation that accumulates spatially and temporally. This is exemplified by the fact that smaller fragments of primary forest have an elevated likelihood of loss (Hansen M. C. et al., 2020). New roads are the primary driver of further degradation as a result of their construction, use, and continued access (e.g., Trombulak and Frissell, 2000; Wilkie et al., 2000; Laurance et al., 2009; Laurance and Balmford, 2013; Ibisch et al., 2016; Alamgir et al., 2017; Venier et al., 2018; Maxwell et al., 2019). Roads render the surrounding forests much more susceptible to agricultural conversion (Asner et al., 2006; Boakes et al., 2010; Gibbs et al., 2010; Laurance et al., 2014; Kormos et al., 2018), logging (Laurance et al., 2009; Barber et al., 2014), and expanded networks of secondary and tertiary roads (Arima et al., 2008, 2016; Ahmed et al., 2014). Logging and transportation can also lead to severe erosion and nutrient runoff, impacting downstream water quality and quantity (Carignan et al., 2000; Hartanto et al., 2003; Foley et al., 2007), and damage the surrounding forest. For example, in the Amazon, it has been estimated that for every commercial tree removed *via* selective logging, roughly 40 m of roads are created, nearly 30 other trees greater than 10 cm in diameter are damaged, and between 600 and 8,000 m^2 of canopy is opened (Holloway, 1993; Asner et al., 2004). Furthermore, roads reduce animal habitat, are barriers to animal movement and lead to increased animal mortality, including from unregulated hunting, all of which decrease connectivity and genetic exchange (Dyer et al., 2002; Frair et al., 2008; Laurance et al., 2009; Taylor and Goldingay, 2010; Clements et al., 2014). One consequence is a decline in carbon-dense tree species due to overhunting of seed-dispersing animals (Osuri et al., 2016; Maxwell et al., 2019). It is important to note that roughly 95% of deforestation in the Amazon occurs within 5.5 km of a road (Barber et al., 2014), and that illegal logging represents 85–90% of all logging in the tropics (Lawson and MacFaul, 2010; Lawson, 2014; Hoare, 2015) and still roughly one-quarter of logging in Russia (Food and Agriculture Organization of the United Nations [FAO], 2012; Kabanets et al., 2013), which contains the largest areal forest coverage of any country (Food and Agriculture Organization of the United Nations [FAO], 2020). Overall, road building and industrial logging are the largest drivers of initial forest degradation and fragmentation (Hosonuma et al., 2012).

In addition to their direct impacts, roads and land use further degrade forests due to edge effects. Forests at or near an edge can have substantially drier microclimates, increased windshear and movement of dry air into forests, invasive species (dispersed *via* roads and more favorable microclimate conditions for competition), weeds and vines, sun exposure, soil erosion, and fuel loads due to drying and previous logging and fire (Laurance and Williamson, 2001; Mortensen et al., 2009; Brando et al., 2014). This leads to a variety of unfavorable impacts and further risks. Carbon densities tend to be significantly lower near forest edges. For example, biomass is reduced by roughly 50% within 100 m, 25% within 500 m, and 10% within 1.5 km of a forest edge (Laurance et al., 1997; Chaplin-Kramer et al., 2015; Maxwell et al., 2019). Aggregated across the tropics, edge effects are estimated to account for up to one quarter of all carbon loss from tropical deforestation (Putz et al., 2014). Primary productivity is also generally lower near forest edges, and fire susceptibility is higher due to elevated and drier fuel loads and increased human access (Laurance et al., 1998; Cochrane et al., 1999; Nepstad et al., 1999; Laurance and Williamson, 2001; Foley et al., 2007; Adeney et al., 2009; Brando et al., 2014). For example, roads are strong predictors of ignition and wildfire frequency in temperate forests (Hawbaker et al., 2013; Faivre et al., 2016; Parisien et al., 2016; Balch et al., 2017; Ricotta et al., 2018), and road expansion in Siberia has been shown to promote logging and human-caused forest fires (Kovacs et al., 2004). A variety of ecosystem services are degraded due to edge effects, including hydrologic regulation, water quality, modulation of regional climate, and amelioration of infectious diseases (Laurance and Williamson, 2001; Foley et al., 2007). Although the impacts are strongest at a forest edge, the effects can generally be detected up to 2 km from the edge, with higher tree mortality up to 1 km and wind disturbance up to 500 m (Broadbent et al., 2008). Globally, fragmentation is thought to be at a critical threshold, with roughly 70% of the world's forest within 1 km of a human-created forest edge (Haddad et al., 2015; Taubert et al., 2018).

Comparison of regenerative capacity

Ecosystem resilience is underpinned by the natural regenerative capacity of a forest ecosystem, and hence represents a major component of ecosystem stability and integrity (**Figure 1**). Regeneration from major disturbance events requires biological legacies, which are broadly defined as the remaining living and dead structures and organisms that can influence recovery (Franklin et al., 2000; Jogiste et al., 2017). These include living and dead trees, shrubs and other plants, seeds, spores, fungi, eggs, soil communities, and living animals (Franklin et al., 2000; Stahlheber et al., 2015; Lindenmayer et al., 2019). Compared to secondary or human-modified forests, primary forests tend to have the biological legacies (Catterall, 2016; Chazdon and Uriarte, 2016; Lu et al., 2016; Poorter et al., 2016; Lindenmayer et al., 2019) and favorable microclimates (von Arx et al., 2013) required for optimal regeneration. This is evidenced by the fact that secondary forest regeneration is aided by proximity to primary forests (Schwartz et al., 2015; Kukavskaya et al., 2016). Clearcut logging also generates low levels of biological legacies and higher regeneration failures after subsequent fires compared to forests not previously logged (Perrault-Hebert et al., 2017), which is exacerbated by post-fire "salvage" logging (Donato et al., 2006; Lindenmayer et al., 2019). Successive disturbances continue to decrease regenerative capacity, and can lead to permanent forest loss and emergence of non-forest ecosystems (Payette and Delwaide, 2003; Johnstone et al., 2016; Kukavskaya et al., 2016). Compared to degraded or human-modified forests, primary forests with large extents also host a much larger array of seed dispersers and pollinators (Muller-Landau, 2007; Wright et al., 2007; Abernethy et al., 2013; Harrison et al., 2013; Peres et al., 2016).

Comparison of biodiversity

Biodiversity underpins and is affected by the foundational elements of ecosystem integrity (**Figure 1**), but is also a metric of ecosystem condition and can be considered an ecosystem service in its own right. Globally, trees are among the most genetically diverse of all organisms, and forests collectively support the majority (roughly 80%) of terrestrial biodiversity (Hamrick and Godt, 1990; Barlow et al., 2007; Pimm et al., 2014; Federici et al., 2017). There is a substantial body of literature on the effects of disturbance and stand age on biodiversity, with some disagreement among studies depending on context (e.g., Paillet et al., 2010; Edwards et al., 2011; Moreno-Mateos et al., 2017; Kuuluvainen and Gauthier, 2018; Matos et al., 2020). Nevertheless, there are clear and definitive negative impacts of human disturbance and land use on biodiversity (Cairns and Meganck, 1994; Ellison et al., 2005; Barlow et al., 2007, 2016; Gibson et al., 2011; Alroy, 2017; Giam, 2017). Primary and ecologically mature forests typically harbor higher biodiversity than human-modified forests (Lesica et al., 1991; Herbeck and Larsen, 1999; Rey Benayas et al., 2009; Zlonis and Niemi, 2014; Miller et al., 2018; Watson et al., 2018; Lindenmayer et al., 2019; Thom et al., 2019), especially in the understory (e.g., Lafleur et al., 2018). Disturbance generally results in a change in species composition toward early pioneer species (e.g., Bawa and Seidler, 1998; Liebsch et al., 2008; Venier et al., 2014). The effect of human activities on the provision of ecosystem services is evident even if there is little change in the overall forest cover. Degradation in logged forests can be in the form of structural changes such as reduction in old age classes of trees that can cause loss in breeding habitat, particularly for birds (Rosenberg et al., 2019; Betts et al., 2022), and compositional changes such as shifts in tree species abundance that differ in foliar nutrient concentrations that support arboreal folivores (Au et al., 2019). Under less intensive agriculture management, agroforestry can maintain a significant fraction of biodiversity, but it is still considerably lower than in native forests (De Beenhouwer et al., 2013; Vallejo-Ramos et al., 2016).

Biodiversity analyses are also strongly dependent on spatial scale, whereby higher levels of management and disturbance homogenize forest composition and age structure across the landscape, and consequently the biota it supports (e.g., Devictor et al., 2008; de Castro Solar et al., 2015; Tomas Ibarra and Martin, 2015). What can be concluded is that (i) degraded and intensively managed forests tend to harbor lower biological and functional diversity compared to primary forests, which support many as yet unidentified species and act as repositories for species that cannot survive in secondary or degraded forests (Barlow et al., 2007; Gibson et al., 2011), and (ii) natural disturbances are effective at maintaining landscape heterogeneity and the species that depend on disturbed and young forests (Lindenmayer et al., 2019). Global biodiversity loss is currently orders of magnitude higher than background rates and is driven primarily by deforestation and forest degradation (Newbold et al., 2016; Giam, 2017). It is worth noting that although natural tree diversity in boreal forests is typically much lower than in temperate or tropical forests (Thompson et al., 2009; Hill et al., 2019), the biodiversity of other species groups such as bryophytes and lichens can be very high (DellaSala, 2011; Kuuluvainen and Gauthier, 2018), functional diversity in boreal forests is generally high (Esseen et al., 1997; Wirth, 2005), and the broad genetic variability and phenotypic plasticity of boreal trees allows them to tolerate a wide range of environmental conditions (Gordon, 1996; Howe et al., 2003).

Comparison of ecosystem condition

Given our focus on climate mitigation, the primary metric of concern for ecosystem condition is carbon stocks. Primary and ecologically older forests have been consistently found to have the highest carbon stocks compared to secondary, degraded, intensively managed, or plantation forests (e.g., Harmon et al., 1990; Cairns and Meganck, 1994; Nunery and Keeton, 2010; Burrascano et al., 2013; Mackey et al., 2013; Keith et al., 2015, 2017; Federici et al., 2017; Lafleur et al., 2018; Watson et al., 2018). For example, a recent meta-analysis shows that primary tropical forests store on average 35% more carbon than forests affected by conventional management for commodity production (Mackey et al., 2020). Across the tropics, intact forest landscapes cover approximately 20% of total area but store 40% of total aboveground biomass (Potapov et al., 2017; Maxwell et al., 2019). This is fundamentally a function of where carbon is stored in these forests. In wet tropical and some temperate primary forests, roughly half the biomass carbon is stored in the largest 1–3% diameter trees (Stephenson et al., 2014; Lutz et al., 2018; Mildrexler et al., 2020), which have long residence times (Koerner, 2017; van der Sande et al., 2017), and are typically the first to be felled (Cannon et al., 1998; Sist et al., 2014; Gatti et al., 2015; Rutishauser et al., 2016). Agricultural landscapes store comparatively less carbon, but the addition of trees *via* agroforestry has the potential to add up to 9 Pg C globally (Chapman et al., 2020). In boreal forests, especially those that are poorly drained, the majority of forest ecosystem carbon is stored in dead biomass, peat, and soil organic layers that accumulate over the course of forest succession, often protected by permafrost (Deluca and Boisvenue, 2012; Bradshaw and Warkentin, 2015; Lafleur et al., 2018; Walker X J et al., 2020). Boreal forests managed for timber are kept at younger ages, with soils that store significantly less carbon due to mechanical disturbance, tree species conversion, and impacts on litter composition, nutrient cycling, and bryophyte communities (Liski et al., 1998; Jiang et al., 2002; Seedre et al., 2014; Lafleur et al., 2018). Even outside the boreal zone, soil carbon can be a significant fraction of total ecosystem carbon (e.g., Keith et al., 2009), and logging activities generally deplete forest soil carbon due to soil compaction and disturbance, erosion, changes in microclimate that increase respiration rates, reduced leaf litter and root exudates, loss of micorrhizal network carbon, and post-logging “slash” burning (Rab, 2004; Zummo and Friedland, 2011; Buchholz et al., 2014; James and Harrison, 2016; Hume et al., 2018; Mayer et al., 2020). Globally, forests are thought to store only half of their potential carbon stock, with 42–47% of the reduction due to forest management and modification (the remainder being deforestation and land cover changes; Erb et al., 2018). Natural regeneration of forests could in turn restore 123 Pg C, or 27% of the total biomass carbon that has been lost (Erb et al., 2018).

Forest management, degradation, and conversion can also result in the loss of key nutrients such as nitrogen and phosphorous, among others, which are otherwise retained efficiently in undisturbed forests (Likens et al., 1970; Markewitz et al., 2004; Olander et al., 2005; Liu et al., 2019). Nutrients can be artificially added, but heavily managed systems require large inputs to maintain their state and productivity capacity (Noss, 1995; Merino et al., 2005; Pandey et al., 2007). Other elements of ecosystem condition are affected similarly and highlighted elsewhere (landscape connectivity / fragmentation in section “Comparison of risks from land use degradation,” biodiversity in section “Comparison of biodiversity,” and water quality and quantity in section “Comparison of ecosystem services”).

Comparison of ecosystem services

A large body of literature indicates the higher number, quality, and value of ecosystem services provided by primary forests compared to human-modified forests and landscapes. These include regulating services such as water quality and quantity (DellaSala, 2011; Brandt et al., 2014; Keith et al., 2017; Kormos et al., 2018; Taylor et al., 2019; Vardon et al., 2019); carbon storage and sequestration as an ecosystem service of global climate regulation (United Nations [UN], 2021) [discussed above, but see Keith et al. (2019) and Uganda Bureau of Statistics [UBOS] (2020) for examples using Ecosystem Accounts]; local to regional biophysical cooling (Spracklen et al., 2012; Lawrence and Vandecar, 2015); regulation of runoff, sediment retention, erosion control, and flood mitigation (Hornbeck and Federer, 1975; Jayasuriya et al., 1993; Dudley and Stolton, 2003; Furniss et al., 2010; van Haaren et al., 2021); provisioning services such as abundance of game and fish (Gamfeldt et al., 2013; Brandt et al., 2014); cultural services such as landscape aesthetics, recreation, and tourism (Brandt et al., 2014; Brockerhoff et al., 2017); cultural practices and knowledge (Normyle et al., 2022); contributions to physical and psychological health (Stier-Jarmer et al., 2021); and general assessments across a suite of services (e.g., Myers, 1997; Harrison et al., 2014; Shimamoto et al., 2018; Maes et al., 2020).

For example, a detailed assessment of the differences between primary forests and post-logging regrowth forests in terms of their ecosystem condition, the physical supply of a suite of ecosystem services, and their monetary valuation showed the superior aggregated value of the primary forest (Keith et al., 2017). The impacts of mechanical disturbance due to logging, roading, and mining on soil properties reduce the ecosystem services of soil nutrient availability, water holding capacity and erosion prevention (Hamburg et al., 2019). A general assessment of the total economic value of ecosystem services provided by forest ecosystem types showed that primary forests had a higher median value (USD 139 ha^{-1} $year^{-1}$) compared with secondary forests (USD 128 ha^{-1} $year^{-1}$) (Taye et al., 2021). These aggregated values include only the market values for services when known and could not account for non-market values, for example that would be needed to assess biodiversity habitat or many cultural services. The highest reported values for specific ecosystem services were for airflow regulation, water cycle regulation and food for freshwater plants and animals. These services would all have their highest provision from natural ecosystems. In contrast, the value of timber and fiber products is significantly lower.

Lessons from comparative analysis

Taken as a whole and for a given set of environmental conditions, our comparative analysis shows that primary forests have the highest levels of ecosystem integrity compared to human-modified forests, including naturally regenerating forests managed for commodity production, plantations, and previously forested landscapes. One primary set of mechanisms are positive feedbacks whereby forest disturbance tends to beget more disturbance (e.g., Seidl et al., 2017), and degradation begets more degradation (e.g., Venier et al., 2018; Watson et al., 2018). In terms of variables most relevant for mitigation, adaptation, and other international forest policy goals, primary forests store the highest carbon stocks, present the lowest risks of forest and carbon loss reversal, have the highest biodiversity, and provide the largest stocks of ecosystem assets and highest quality flows of ecosystem services, including benefits to the global community, local communities (Vickerman and Kagan, 2014), and Indigenous peoples.

Based on our review, and because human-modified forests can encompass a wide range of management strategies and intensities, we provide further summaries of ecosystem integrity for five main categories of forest types: (A) primary forests; (B) secondary forests; (C) production forests; (D) agro-forests; and (E) plantations (**Figure 2** and **Table 1**). Primary forests have the most developed dissipative structures, the highest levels of ecosystem processes, greater stability and recovery, and thus greater resilience and the lowest risk of loss and damage. As defined here, secondary forests are in recovery from past human impacts especially logging. Although they can transition to primary forests over time, these forests lack some old growth characteristics, are more vulnerable to wildfire and other natural disturbances, and have missing elements of biodiversity. Production forests are a result of conventional forest management for commodity production, and tend to be kept at relatively young ages with associated reductions in dissipative structures, carbon stocks, and resilience. An example of commercial agro-forests is shade coffee where retaining some natural canopy tree cover provides some additional ecosystem service benefits. Subsistence agro-forests are common in many tropical development countries such as Vanuatu where these household and community gardens were, and in many cases still are, the main source of food. Commercial plantations include monocultures of trees species that are essentially tree farms for commodity production (wood, palm oil). Note that there are gradients of human modification, stand age, and ecosystem integrity within these broad categories. For example, mature forests recovering from past human disturbances may not have the full suite of structural, functional, and compositional benefits as primary forests, but they can gain these over time, and generally have higher ecosystem integrity than forests

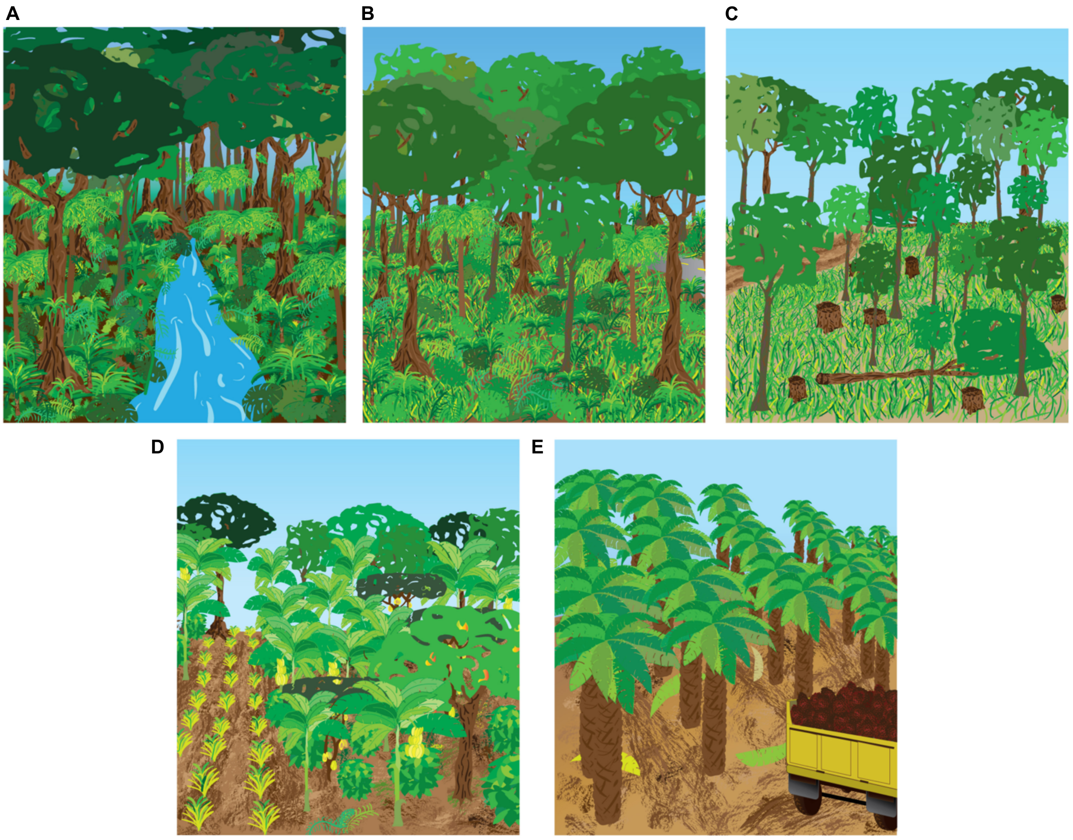

FIGURE 2
Graphical illustrations of five main forest types considered for ecosystem integrity comparisons, including **(A)** primary forests, **(B)** secondary forests, **(C)** production forests, **(D)** agro-forests, and **(E)** plantations. Note this illustration focuses on tropical forests, but the same general differences apply across forest biomes.

TABLE 1 Comparison of ecosystem integrity foundational elements between five main forest types.

Primary forest

- Naturally regenerated forest of native tree species, where there are no clearly visible indications of human activities and the ecological processes are not significantly disturbed
- Likely to have never been commercially logged or intensely managed
- At a landscape level, can comprise early successional (seral) stage following natural disturbances
- More likely to contain full complement of evolved natural biodiversity
- Often the customary territories of Indigenous Peoples

Dissipative structures	● *Ecosystem processes*	● *Stability and risk profiles*	● *Ecosystem integrity level*
● Canopy trees dominated by large, old trees ● In wet tropics, closed canopies ● Dense soil organic stocks ● Typically significant quantities of dead biomass	● Fully self-generating (autopoiesis) ● In temperate and boreal forests, includes seral stages following natural disturbances ● Tight nutrient cycling with minimal leakage and/or erosion ● Clean water supply	● Highly resistant and/or resilient to extreme weather events ● In boreal and temperate biomes, fire-adapted plant species ● Rich biodiversity provides functional and phenotypic adaptive capacity	● High levels for all three factors

Secondary forest

- Natural forests recovering from prior human land use impacts
- Canopies dominated by pioneer and secondary growth tree species
- If not subsequently disturbed by human land use, can continue to develop additional primary forest attributes over time

● *Dissipative structures*	● *Ecosystem processes*	● *Stability and risk profiles*	*Ecosystem integrity level*
● In wet tropics, canopy closure can occur within 1–2 decades ● Aboveground living significantly less than primary forests ● Some dead biomass may remain	● Fully self-regenerating so long as primary propagules/seed stock are available ● Soil carbon and nutrients stocks can be depleted due to past erosion and biomass removal	● In temperate and boreal forests, increased exposure to wildfire and drought impacts due to more open canopy and drier forest interior ● Reduced biodiversity impairs some key processes (e.g., pollination, top-down tropic control)	● Moderate depending on time since disturbance

Production forest

- The consequence of conventional forest management for commodity production (e.g., timber, pulp)
- Forest predominantly composed of trees established through natural regeneration, but management favors commercially valuable canopy tree species

● *Dissipative structures*	● *Ecosystem processes*	● *Stability and risk profiles*	*Ecosystem integrity level*
● Logging regimes maintain a predominantly even-aged, younger age structure (~20–60 years) ● Simplified vertical vegetation structure	● Canopy tree species natural regenerated but some level of assisted regeneration common ● Ongoing soil loss	● More flammable forest conditions ● Greater exposure to invasive species	● Low to moderate depending on intensity of logging regimes and biodiversity loss

Agro-forestry (commercial, subsistence)

- Some level of natural tree species is maintained with subsistence food or commercial crops grown (e.g., shade coffee).
- Swidden subsistence farming commonly used by traditional communities
- Utilizes a mix of natural and assisted regeneration

Dissipative structures	*Ecosystem processes*	*Stability and risk profiles*	*Ecosystem integrity level*
● A curated canopy of trees, often remnant from primary forest or planted from local stock ● Little if any understory ● Ground cover are food crops	● In tradition swidden system, closed nutrient cycle through use of natural regeneration ● Canopy trees buffer food crops from extreme weather and help maintain soil moisture	● Intensive small-scale management and modest level of biodiversity provides assisted resilience and adaptive capacity	● Low to moderate given sufficient management inputs

(Continued)

TABLE 1 (Continued)

Commercial plantation

- Forest predominantly composed of trees established through planting and/or seeding and intensely managed for commodity production (timber, pulp, plant oil)

Dissipative structures	*Ecosystem processes*	*Stability and risk profiles*	*Ecosystem integrity level*
• Typically mono-cultures that are harvested at around a young age (~10–20 years)	• Soil water and nutrient retention • Can utilize natural pollinators from neighboring or remnant natural forests	• Exposed to extreme weather events, invasives, pests, and disease • Intensive large-scale management needed	• Low

recovering from more recent human disturbance (DellaSala et al., 2022b).

Implications for policy, management, and future research

Evaluating ecosystem integrity

We have shown that the risk of forest carbon loss can be minimized by prioritizing actions that maintain and enhance forest ecosystem integrity. Ecosystem integrity therefore has the potential to be used as an integrating framework for evaluating forest-based mitigation and adaptation actions. Because ecosystem integrity is an inherently complex concept, the scientific, management, and policy communities need approaches and tools to measure and interpret gradients of integrity consistently across forest types and jurisdictional boundaries (Karr, 1996; Grantham et al., 2020). The metrics and their interpretation should ideally account for the range of spatial and temporal scales involved: small patches of high-integrity forests are valuable, but landscape context is required; snapshots in time are useful, but longer-term dynamics are needed to fully understand integrity.

A complete and exhaustive global representation of forest ecosystem integrity may currently be beyond our reach. Nevertheless, several existing data products represent important elements of ecosystem integrity, each with their own advantages and limitations, and can be used to guide decision making. In the humid tropics, natural and hinterland forests (primary forests and mature secondary growth) have been mapped using multispectral satellite imagery (Turubanova et al., 2018) and spatial statistics (Tyukavina et al., 2016). Canopy structural integrity has recently been mapped using space-based lidar, multispectral imagery, and human pressure indices (Hansen et al., 2019; Hansen A. J. et al., 2020), representing an important step in delineating gradients of integrity. These mapping approaches are inherently more challenging outside the humid tropics where environmental gradients generate a range of potential forest cover and types. Global products therefore tend to rely more on metrics based on the relationships between forest loss/degradation and proximity to human activities, including roadless areas, forest fragmentation, loss of tree cover, and measures of the "human ecological footprint" (Hansen et al., 2013; Haddad et al., 2015; Ibisch et al., 2016; Venter et al., 2016b,a; Beyer et al., 2020; Grantham et al., 2020; Williams et al., 2020). Global Intact Forest Landscapes (Potapov et al., 2008, 2017) have been widely used, but these include patches of non-forest ecosystems and exclude areas of high-integrity forests in patches <50,000 ha. The Food and Agriculture Organization of the United Nations (FAO) has reported on primary forests since 2005 in their global forest assessment reports (Food and Agriculture Organization of the United Nations [FAO], 2020), but a lack of consistency in national-level reporting makes comparisons and trend detection difficult.

Similar to Grantham et al. (2020), we stress the importance of using local data and field observations to further identify and refine estimates of forest ecosystem integrity derived from coarser-scale global mapping products. These may include landscape-level metrics such as frequency distributions of stand age, biomass, coarse woody debris, biodiversity, forest patch sizes and shapes, and forest types and species composition. Individual countries have data archives, collection programs, and often agency directives that either include ecosystem integrity metrics or those with high relevance for integrity assessments (e.g., Muller et al., 2000; Tierney et al., 2009; Wurtzebach and Schultz, 2016). Applying the internationally endorsed SEEA-EA system should also enable a consistent framework for comparisons across spatial and temporal scales. The SEEA-EA standard provides guidance for classifications, definitions, spatially explicit analysis, and temporal consistency. Technical guidance on ecosystem integrity indicators was recently provided by Hansen et al. (2021). Although criteria were provided in the context of CBD's post-2020 Global Biodiversity Framework, many would apply outside this context, including a need for biome to global scale products with spatial resolution sufficient for management ($\leq$ 1 km), temporal re-assessment at intervals of 1–5 years, ability for indicators to be spatially aggregated without bias, credibility through validation and peer review, and accounting for reference states within a given climate, geomorphology, and ecology. Finally, we note the importance of understanding how any given metric of ecosystem integrity connects to the conceptual framework of ecosystem integrity (**Figure 1**).

Implementing ecosystem integrity

Protecting primary forests

Given the superior benefits of primary forests, follows that protecting them would significantly contribute to meeting international climate, biodiversity, and SDGs. Primary forests are disappearing at a rapid rate (e.g., Potapov et al., 2017; Food and Agriculture Organization of the United Nations [FAO], 2020; Hansen M. C. et al., 2020; Silva Junior et al., 2021) and urgently need higher levels of protection to ensure their conservation; only roughly one-fifth of remaining primary forests are found in the International Union for Conservation of Nature (IUCN) Protected Areas Categories I-VI (Mackey et al., 2015). Proven effective mechanisms to protect primary forests include enforcing existing and establishing new reserves and protected area networks, limiting new road construction, payments for ecosystem services, effective governance, and protecting the rights and livelihoods of indigenous peoples and local communities (Mackey et al., 2015; Kormos et al., 2018; Walker W. S et al., 2020). Complementary measures and enabling conditions include supporting legislation and enforcement of protection status, industry re-adjustment to source alternative fuel, food and wood products, and management of weeds, pests, feral animals, and livestock grazing (Mackey et al., 2020).

Protecting primary forests will also be facilitated by changes to current international forest and carbon accounting rules. Existing “net” forest cover accounting rules, such as the IPCC good practice guidelines for national greenhouse gas inventories and the land sector, are problematic because they report net changes and treat all forests equally, regardless of their integrity, thereby incentivizing the conversion of primary forests into commodity production (Mackey et al., 2013, 2015; Peterson and Varela, 2016; Moreno-Mateos et al., 2017; Funk et al., 2019; Skene, 2020). Such changes in forest management can have the perverse effect of accelerating emissions and degrading ecosystems. Similarly, flux-based carbon accounting effectively hides the emissions or lost sequestration potential from logging primary forests (e.g., Skene, 2020) and does not account for the risk profiles of different forest types. Reporting “gross” forest cover changes as well as adopting stock-based accounting (Ajani et al., 2013; Keith et al., 2019, 2021) could more fully leverage an ecosystem integrity framework, and ultimately ensure the maximum mitigation benefits and ecosystem services are secured from Earth’s remaining forests.

Management of other forest types

Management of secondary forests for commodity production, along with tree plantations and agroforestry, can contribute to climate mitigation and other SDGs and reduce pressure on primary forests and other natural forests with high levels of ecosystem integrity (Watson et al., 2018; Roe et al., 2019; Chapman et al., 2020). However, the key is to direct these management activities to previously deforested or degraded lands and accompany them with systematic landscape planning and effective governance (Dooley et al., 2018; Kormos et al., 2018; Martin et al., 2020; Morgan et al., 2020). For example, much of the overall timber demand could be harvested from secondary forests, but these are often overlooked as resources by land owners, the timber industry, and governments (Bawa and Seidler, 1998). Globally, intensively managed tree plantations or planted forests supply over 50% of global wood supply (Warman, 2014) yet occupy only 7% of global forest cover (Food and Agriculture Organization of the United Nations [FAO], 2020). It is therefore feasible to meet global wood supply with existing plantations and additional ones established on previously cleared or degraded land. These land uses, however, are decidedly not beneficial for carbon budgets or ecosystem services when undertaken at the cost of clearing or degrading primary forests.

Governments and forest managers can aim to optimize the ecosystem integrity of secondary forests (for example in terms of yield, regenerative capacity, and biodiversity) within the confines of their intended uses (Thompson et al., 2009; Grantham et al., 2020). In tandem with alternative fibers, this will help alleviate pressures on primary forests. A similar argument exists for agricultural productivity (Laurance et al., 2001; Hawbaker et al., 2006; Sabatini et al., 2018). All of these activities can be done with appropriate landscape planning in ways that collectively increase economic yield and ecosystem services, and serve local communities (Bawa and Seidler, 1998; Burton et al., 2006; Mathey et al., 2008; Food and Agriculture Organization of the United Nations [FAO], 2012; Naumov et al., 2016).

Afforestation, forest restoration, and proforestation (i.e., allowing secondary forests to naturally regrow and restore their ecosystem carbon stocks) are also important components of forest-based mitigation and conservation activities (Giam et al., 2011; Griscom et al., 2017; Verdone and Seidl, 2017; Moomaw et al., 2019; Roe et al., 2019; Cook-Patton et al., 2020). Proforestation holds promise for near-term mitigation because the established trees are already on the steepest part of their growth curve (Moomaw et al., 2019; Mackey et al., 2020). However, none of these forest management activities can replace the carbon stocks and ecosystem services of high-integrity primary forests on decadal to century timeframes. It is also generally less expensive to protect primary forests than to reforest or restore forests (Possingham et al., 2015; Griscom et al., 2017). Furthermore, potential “overcrediting” for offset and restoration schemes can result in net harm and carbon emissions, whereas “overcrediting” for primary forest protection only reduces the benefits, but does not lead to net societal and climate damages (Anderegg et al., 2020). We therefore urge that forest restoration should be conducted in concert with protection of primary forests, and not instead.

Finally, we note that selective logging, or so called "reduced impact logging" in tropical forests has been shown many times to be unsustainable (Zimmerman and Kormos, 2012; Kormos et al., 2018), as it results in significant damage to the target forests as well as collateral damages to surrounding forests due to road building, transportation, and further clearing for land uses such as agriculture (Kormos and Zimmerman, 2014; Mackey et al., 2020). Generally, as timber extraction becomes less intensive, the per-tree collateral damages increase exponentially (Gullison and Hardner, 1993; Boot and Gullison, 1995; Bawa and Seidler, 1998; Umunay et al., 2019; Zalman et al., 2019). After the first cut, selective logging is much less economically viable compared to plantations and intensive forestry (Bawa and Seidler, 1998; Naumov et al., 2016). Even measures aimed at reducing emissions *via* collateral damages from selective logging may not generate benefits and merely serve to justify and subsidize the degradation of high-integrity primary forests (Macintosh, 2013; Watkins, 2014; Gatti et al., 2015). Overall, selective logging and its associated degradation may be as much or more harmful than outright deforestation for pan-tropical forests and their carbon stocks (Nepstad et al., 1999; Foley et al., 2007; Baccini et al., 2017; Erb et al., 2018; Bullock et al., 2020; Matricardi et al., 2020).

Relevance for international policy

There has been a recent uptick in the recognition of the importance of ecosystem integrity and primary forests for multiple climate, biodiversity, and SDGs. For example, the preamble to the Paris Agreement notes the importance of ensuring the integrity of all ecosystems, and recent international policy developments point to the importance of maintaining and restoring ecosystem integrity for achieving the goals of the Rio Conventions and all of the SDGs, but in particular SDG 15 (Life on Land). The importance of primary forests for achieving synergistic climate and biodiversity outcomes was also reflected in Working Group II (IPCC, 2022) and III (Nabuurs et al., 2022) of the IPCC's Sixth Assessment Report, as well as key decisions from the CBD 14th Conference of the Parties (14/5 and 14/30) (Convention on Biological Diversity [CBD], 2018).

We strongly recommend an increased focus on integrating climate and biodiversity action, which provides an opportunity to deliver multiple societal goals through ensuring the integrity of ecosystems (Barber et al., 2020). The importance of the nexus between effective action on climate change and biodiversity is reflected in the findings of the first ever joint workshop of the IPCCC and IPBES held in 2021 (Pörtner et al., 2021), which encouraged synergistic climate and biodiversity action and identified priorities for action, in particular the protection and restoration of carbon and species rich natural ecosystems such as forests.

The integrity of ecosystems is also being promoted by civil society as an important factor to consider in the UNFCCC Global Stocktake, a central pillar of the Paris Agreement against which its success or failure will be judged (Climate Action Network, 2022). We suggest that utilizing the UN SEEA-EA to benchmark protection and restoration actions would provide critical information on ecosystem integrity elements for the Global Stocktake to inform high-benefit / low-risk nature-based solutions in evolving NDCs. Successful implementation of the ecosystem provisions of the UNFCCC and the Paris Agreement, including decisions made at COP 25 (1.CP 25 para. 15) calling for integrated action to prevent biodiversity loss and climate change; and COP 26 (CMA/3 para. 21 and 1.CP/26 para. 38) emphasizing "...the importance of protecting, conserving and restoring nature and ecosystems, including forests ...," depends upon understanding the significance of ecosystem integrity for stable long term carbon storage and the overall health of the biosphere.

Other recent policies and guiding documents include the Glasgow Leaders' Declaration on Forests and Land Use (United Nations Climate Change, 2021), CBD post-2020 Global Biodiversity Framework (Convention on Biological Diversity [CBD], 2021), IUCN Policy Statement on Primary Forests Including Intact Forest Landscapes (IUCN, 2020), IPBES Global Assessment Report (IPBES, 2019), the New York Declaration on Forests 5-Year Assessment Report (NYDF Assessment Partners, 2019), the European Parliament resolution to protect and restore forests (European Parliament, 2020), and Indonesia's moratorium on converting primary forests and peatlands (Austin et al., 2019).

Nevertheless, there is still much work to be done at national and international levels, with the evolving Paris Rulebook and country NDC's arguably representing the largest opportunity. Translating all these international declarations into coherent national and jurisdictional policies will require an agreed-upon framework of ecosystem integrity, such as provided here, and applicable data products tools for implementation.

Future research directions

Because ecosystem integrity is such an integrative and multidisciplinary concept, research gaps are relatively extensive. We therefore do not offer an exhaustive list, but rather a prioritized assessment of future research directions to improve the understanding, valuation, and operationalization of ecosystem integrity. First and foremost, operationalizing forest ecosystem integrity at scales relevant to policy and planning that span from landscape planning (Morgan et al., 2022) to national strategies (Center for Biological Diversity [CBD], 2022) and international agreements (United Nations [UN], 2021) requires accurate and updated maps of ecosystem integrity and its components. Existing products (described in section "Evaluating ecosystem integrity") touch on aspects of canopy structural integrity, can be used to identify areas of remaining natural forests, and, using time series data, can locate where they have been lost (**Figure 3**). However, their ability to differentiate levels of integrity between forests is limited, and they do not account for the longer-term ecosystem dynamics that comprise functional integrity. It will therefore be helpful to leverage the time series of now decades-long satellite records such as Landsat and the Moderate Resolution Imaging Spectroradiometer (MODIS) to incorporate metrics of stability / resistance, and to capture smaller patches of high-integrity forests, such as in Shestakova et al. (2022). In boreal and temperate forests with naturally occurring stand-replacing disturbances, for example wildfire, it will be critical to accurately separate these from human disturbances, for example by using spatial pattern recognition techniques (e.g., Curtis et al., 2018).

For the purpose of primary forest protection, accurate maps of regularly updated primary forests are needed at sufficient spatial scales and accuracy to support both country-level assessments as well as local decision making. Spatial assessments of forest ecosystem integrity and components, as opposed to categorical maps of forest/no-forest or broad forest types, are particularly needed. In addition to developing countries, this information is needed in the United States, Europe, and other developed countries with little remaining primary forests. In these cases, the most ecologically mature forests for a given ecosystem type (e.g., DellaSala et al., 2022b) likely represent the highest integrity levels rather than primary forests per se (**Table 1** and **Figure 2**) and similarly require both field and remote sensing analysis to be defined and identified (e.g., Federal Register, 2022). Aside from mapping methodologies and data products, we stress the need for continued and new field monitoring programs that evaluate and track ecosystem integrity components as they are impacted by climate and human land use at various scales.

More focused scientific studies on the components of ecosystem integrity as described here (**Figure 1**) are needed to better define, quantify, and monitor integrity in different ecoregions. For example, we know relatively little about how biodiversity and ecosystem composition in many forested regions globally is responding to the combined impacts of climate change, landscape fragmentation, and land use, nor how these will continue to evolve in the future. Such understanding would facilitate management decisions to increase ecosystem integrity or limit its decline, which is particularly important for managing future risks and vulnerability of carbon stocks in the context of carbon markets and offsets (Anderegg et al., 2020). Developing methods for comprehensive yet transferable ecosystem service valuations are particularly important for both scientific understanding as well as conservation mechanisms such as Payments for Ecosystem Services and the UN System of Environmental Ecosystem Accounting.

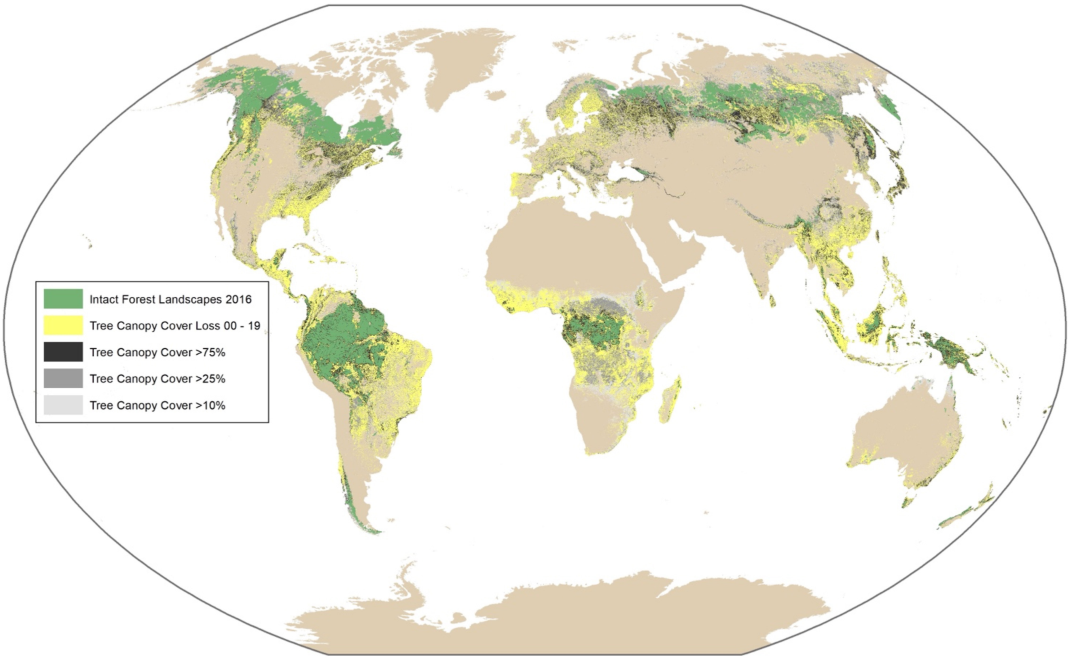

FIGURE 3
Global forest condition as indicated by metrics of Intact Forest Landscapes (IFLs), tree canopy cover, and tree canopy cover loss (from 2000 to 2019). IFLs for the year 2016 are taken from Potapov et al. (2017), and tree cover and tree cover loss outside of IFLs are from Hansen et al. (2013).

Finally, we suggest prioritizing research that optimizes the distribution of secondary forest management, including intensive plantations, to alleviate the pressure on primary and high integrity natural forests worldwide, as well as policy mechanisms needed for incentivization. Such research needs to account for regionally varying economic and equity issues in order to be effective.

Conclusion

In this paper we reviewed the components, importance, and potential for ecosystem integrity to help guide international forest policy and foster greater policy coherence across the climate, biodiversity, and sustainable development sectors. Our operating framework for forest ecosystem integrity encompasses biodiversity, dissipative structures, ecosystem processes, ecosystem stability, and the resulting ecosystem condition and services. A comparative analysis showed that, compared to forests with significant human modification, primary forests generally have higher ecosystem integrity and thus lower risk profiles for climate mitigation.

The scientific and management communities need better tools to accurately forecast the risks associated with different forest ecosystems, particularly those being managed for natural climate solutions and mitigation (Anderegg et al., 2020). Given these tools may be years or more away, we suggest focusing on ecosystem integrity is an optimal solution for categorizing forest-based risks and protecting ecosystem services. Doing so would (i) optimize investment in land carbon stocks and mitigation potential, (ii) identify stocks that provide the best insurance against risk of loss, and (iii) ensure the highest levels of benefits from ecosystem services, thereby optimizing compatibility and synergy between mitigation, adaptation, and SDGs. A number of large-scale data products exist to guide this focus. Nevertheless, there are substantial remaining gaps in terms of understanding, mapping, monitoring, and forecasting forest ecosystem integrity and its components in the midst of increasing human pressure and climate changes. Because primary forests have a higher level of ecosystem integrity than forests managed for commodity production, plantations, or degraded forests, we stress the continuing and increased need for their protection. An effective strategy is to create high carbon density strategic carbon and biodiversity reserves that include primary forests and recovering secondary forests that are quickly accumulating carbon (Law et al., 2022).

Author contributions

BR, BM, VY, and HK conceived the study. BR, BM, and HK led the writing, with contributions from CK, DD, GB, JD, RH, RB, TS, VY, and WM. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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