Landscape Ecology

Evaluating Climate-Driven Fallowing for Ecological Connectivity of Species at Risk

--Manuscript Draft--

Manuscript Number:	LAND-D-22-00067R2
Full Title:	Evaluating Climate-Driven Fallowing for Ecological Connectivity of Species at Risk
Article Type:	Original research
Keywords:	Conservation planning; dynamic reserves; agricultural matrix; endangered species; connectivity; drought
Corresponding Author:	Sofie HE McComb The University of British Columbia Vancouver, British Columbia CANADA
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	The University of British Columbia
Corresponding Author's Secondary Institution:	
First Author:	Sofie HE McComb
First Author Secondary Information:	
Order of Authors:	Sofie HE McComb
	L. Claire Powers
	Ashley Larsen
Order of Authors Secondary Information:	
Funding Information:	Faculty of Graduate Studies, University of British Columbia — Ms. Sofie HE McComb
	BioFrontiers Institute, University of Colorado Colorado Springs — Ms. L. Claire Powers
	National Science Foundation (2042526) — Dr. Ashley Larsen
	U.S. Department of Agriculture (2022-67019-36397) — Dr. Ashley Larsen

Abstract:

Context

Climate change and agricultural land use change are modifying the configuration of natural lands within agricultural landscapes, impacting species’ ability to move freely between remaining (semi-)natural areas. Working lands are inherently costly to set aside for biodiversity, making the establishment of additional permanent reserves that facilitate connectivity challenging.

Objectives.

Here we explore the potential for dynamic conservation reserves, in the form of either temporarily or semi-permanently fallowed croplands, to increase connectivity in intensive agricultural regions.

Methods

We perform landscape connectivity analyses to examine how drought-induced fallowing between 2011 and 2017 may have impacted connectivity within Kern County for the endangered San Joaquin kit fox (Vulpes macrotis mutica).

Results

We found that an increase in fallowed lands from 2011 to 2015/2017 in Kern County likely corresponded to increased connectivity for the kit fox, including significant decreases in cumulative cost to distance traveled (~0.8–18% and 0.3–12.2% in 2015/2017 respective to 2011 across model scenarios). These significant reductions indicate that cumulative energy costs incurred by kit foxes traveling between core habitats likely decreased with an increase in fallowing, with the estimated benefits from semi-permanently fallowed lands on average 2.4 times greater than for more

	temporarily fallowed. Conclusions Our results highlight that dynamic conservation actions have the potential to reduce conflict between biodiversity preservation and agricultural production in working landscapes by increasing landscape connectivity via temporarily or semi-permanently fallowed parcels. Agri-environmental programs incentivizing the creation of dynamic, fallowing-based reserves could help landowners manage reduced groundwater availability while improving species' mobility under climate change.
Response to Reviewers:	Response to Editor COMMENTS FOR THE AUTHOR: Dear Dr. McComb, Thank you for your submission "Evaluating Climate-Driven Fallowing for Ecological Connectivity of Species at Risk." This article is looking very good. Thanks for all the work that you have done in this interesting and well-written research. I have two small last suggestions and then I believe it is ready for publication. Thank you so much for all your help and support throughout this process. The main takeaway seems to me to be that drought and policy-driven fallowing results in increased fallowing. The dynamic nature of the fallowing seems less clear in the study. I believe the manuscript has moved to clarify these conclusions. Thank you. Modeling habitat with two separate (idle vs retired) fallow scores is a good response to reviewer's apt concern that it is self-fulfilling that, by definition, setting a higher suitability score for fallowed lands, will automatically result in outputs that have increased connectivity. Please make sure this comparison and results are prominently presented. Consider including in the abstract (these results are not mentioned now) a statement like "the benefits were on average more than 2.5 times greater with longer-term fallowing." Could you also please take a last look at the use of temporary in the article and confirm that it is consistent with your final revised message? Thank you so much. We have ensured that all results are now presented clearly and consistently throughout the paper, particularly between the two fallowing scenarios. We have further highlighted the comparison between shorter-term, transitory idle fallow lands and longer-term, semi-permanent retired fallow lands throughout the paper. We have added a few lines throughout the results section highlighting the differences in shorter versus longer term fallowing results for each metric and across metrics (Lines 482-485, 494-496, 509-515), and then included a line in the abstract (Lines 56-59) and updated the relevant lines in the discussion (Lines 560-561, 639-644) to further support that comparison. We have updated or removed the use of the word temporary throughout—often with the use of the words temporarily or transitory—to hopefully better reflect the final message and the difference between the two fallow scenarios, both of which can be dynamic and temporary in a sense, but one of which is of a longer and more semi-permanent duration (retired) than the other (idle). Secondly, while I greatly appreciate your response to reviewers' requests for additional background review, the reference list has become a bit bloated. And there still is a relatively high proportion of articles that are ~20 years old. Can you take one last look through and update/assess essentialness of references especially where have long daisy-chain lists of references at the end of some of your points. We agree, and have done our best to go through each of the references, and parse down the citations where possible throughout. We have had to leave some of the relevant kit fox articles from the 90's as they were pivotal kit fox tracking or land-use studies, but otherwise we have tried to ensure studies cited are as recent and relevant as possible. I have added a few small points below. I look forward to receiving your final draft. Thank you again for your work on preparing this paper. Thank you again for your suggestions, and we have addressed the rest of the specific revisions below.

Best,
Todd Lookingbill
Coordinating Editor

Line 48: Should temporary be used here, as the results are for temporary idle or permanently retired lands?
We have removed the use of the word temporary here (Line 53), as you are correct the results presented are for both, and the word may increase confusion. We have also removed the use of the word throughout the paper in areas where it may cause confusion.

Line 50: "(~0.8–18% and 0.3–12.2% in 2015/2017 respective to 2011" Please provide a brief explanation for the range of values presented, even if simply "for different model scenarios."
We have added "across different model scenarios" to clarify results presented (Line 56).

Line 58: Awkward sentence: "Fallowing-based, agri-environmental programs could help support landowners manage reduced groundwater availability"
We agree and have changed the sentence to read (Lines 65-67): "Agri-environmental programs incentivizing the creation of dynamic, fallowing-based reserves could help landowners manage reduced groundwater availability while improving species' mobility in the face of climate change."

Lines 71 and 111: change "high value" to "high-value"
Changed to "high-value" (Lines 76 & 113).

Line 86: add comma after "Interestingly"
Added comma after "Increasingly" in this line (now Line 91).

Line 149: delete "also" as it is used in the sentence above
Deleted "also" (Line 151).

Figure 1 caption: add "and" before "2017".
Added "and" (Line 230).

Line 333 and 334: insert space between "Eq." and "5".
Inserted the space (Line 338).

Results: There is an occasional shift from past to present tense - e.g., lines 421-425, 465
We read through the results section and ensured all appropriate verbs were in past tense (Lines 419-521). The only lines left in present tense were Lines 465-467—"Thus, while these summaries illustrate overall trends in mobility across the landscape, they do not account for the paired nature of pathways between any given core areas."—as we believe they were more appropriately phrased this way, but we can change to past tense if needed.

Figure 4 is slightly more difficult to interpret now that it is a two-panel figure. Consider making the top row "retired" and the bottom row "idle," that would make it easier to compare the same metrics across scenarios. Also consider keeping the y-axes consistent between the retired and idle scenarios to allow for easier comparison.
Thank you for the suggestion, and we have altered the figure to have the idle results on the top row, and the matching retired results on the bottom row, with consistent y-axes, for ease of direct comparison.

Discussion - it strikes me that the reduction in amount of fallowed land from 2015 to 2017 is one of the main pieces of evidence about the "dynamic" nature of the fallowing. Is "retired" land still dynamic. Please review your use of dynamic throughout.
We agree and have ensured the use of "dynamic" is consistent throughout and that it corresponds with the definition we included in the introduction (Lines 115-116, "adaptively managed protected areas with spatial distributions that change through time based on environmental impacts to biodiversity and agricultural production"). We

	have made sure to clarify in the methods section that retired fallow lands represents longer duration of fallowing than idle, but that both can be used dynamically as the retired fallowing scenario is just longer-term and more semi-permanent than the idle fallowing scenario, resulting in increased recovery and overall suitability from the extended length of fallowing. For instance, a parcel of farmland could be retired for a few years to support connectivity and other ecological benefits, but could later be exchanged with another parcel if that were to improve the spatial arrangement of connectivity corridors due to an alteration in climate, land use, or species condition. We have changed the paragraph describing retired versus idle scenarios to reflect this (Lines 299-310): “Since the difficulty of traversing fallowed land may differ based on the duration of fallowing (Cypher et al., 2007), we evaluate two different suitability scenarios. First, we consider the suitability of all fallowed lands as "retired", or fallowed for more than one year, to mimic what we might expect in a drought or under SGMA, in which fallow lands are assumed to more closely resemble grassland or shrubland due to a longer duration of fallowing and therefore increased vegetative recovery and habitat suitability in these semi-permanent areas (Cypher et al., 2007, 2013). Second, we evaluated fallowed lands as "idle", or fallowed for one year, in which they are assumed to more closely resemble barren land due to the shorter-term and more transitory nature of fallowing (Cypher et al., 2013). As the distribution of fallowed lands from 2011 to 2017 was likely a combination of these land types, we chose to evaluate these two suitability scenarios to bound our results. Results associated with these two types of fallow land are hereafter referred to as ‘retired’ and ‘idle’ results, respectively.” We consider both longer-term, semi-permanent fallowed lands and shorter-term, transitory fallowed lands as potential areas for dynamic connectivity reserves, and Lines 646-649 in the discussion try to highlight this point: “Though the opportunity costs of fallowing to farmers under SGMA will likely be high, those costs have the potential to be partially offset by tapping into the conservation potential of dynamic reserves and conservation corridors comprised of either temporarily and/or semi-permanent fallowed lands.” Line 613: should “layer” be “layers”? Changed to “layers” (Line 630).

Evaluating Climate-Driven Fallowing for Ecological Connectivity of Species at Risk

Sofie McComb[1,2]*, Claire Powers[1,3], Ashley Larsen[1]

[1]Bren School of Environmental Sciences and Management, University of California Santa Barbara, United States
[2]Department of Forest and Conservation Sciences, Faculty of Forestry, University of British Columbia, Canada
[3]Environmental Studies and Interdisciplinary Quantitative Biology Programs, University of Colorado Boulder, United States

***Author to whom correspondence should be addressed:**
Sofie McComb
Department of Forest and Conservation Sciences, University of British Columbia
6201 Cecil Green Drive #321
Vancouver, BC V6T 1Z1
Canada
Telephone: +1 (281) 435-4865
Email: shemccomb@gmail.com
ORCID: 0000-0003-2237-1833

Keywords: conservation planning, dynamic reserves, agricultural matrix, endangered species, connectivity, drought

Acknowledgements

We thank Forrest Melton at the NASA Ames Research Center Cooperative for Research in Earth Science and Technology and NASA Applied Sciences Program and Western Water Applications Office for sharing the NASA-USGS-USDA Fallowed Area Mapping (FAM) project data and providing comments on this manuscript. Additionally, we would like to thank our editor and all of our reviewers for their thorough and constructive comments, which helped us to improve the quality of this manuscript.

Abstract

Context.

Climate change and agricultural land use change are modifying the configuration of natural lands within agricultural landscapes, impacting species' ability to move freely between remaining (semi-)natural areas. Working lands are inherently costly to set aside for biodiversity, making the establishment of additional permanent reserves that facilitate connectivity challenging. Yet, even temporary increases in connectivity may enable increased gene flow with long-term benefits for species health and persistence.

Objectives.

Here we explore the potential for dynamic conservation reserves, in the form of either temporarily or semi-permanently fallowed croplands, to increase connectivity in intensive agricultural regions.

Methods.

We evaluate the potential for fallowed lands to facilitate functional habitat connectivity for an at-risk species in the San Joaquin Valley, an intensive agricultural landscape in California, USA. We perform landscape connectivity analyses to examine how drought-induced fallowing between 2011 and 2017 may have impacted connectivity within Kern County for the endangered San Joaquin kit fox (*Vulpes macrotis mutica*).

Results.

We found that an increase in fallowed lands from 2011 to 2015/2017 in Kern County likely corresponded to increased functional connectivity for the kit fox, including significant decreases in cumulative cost to distance traveled (~0.8–18% and 0.3–12.2% in 2015/2017 respective to 2011 across different model scenarios). These significant reductions indicate that cumulative energy costs incurred by kit foxes traveling between core habitats likely decreased with an increase in fallowing, with the estimated benefits from semi-permanently fallowed lands on average 2.4 times greater than for more temporarily fallowed lands.

<u>Conclusions.</u>

Our results highlight that opportunistic and dynamic conservation actions have the potential to reduce conflict between biodiversity preservation and agricultural production in working landscapes by increasing landscape connectivity via temporarily or semi-permanently fallowed parcels. Agri-environmental programs incentivizing the creation of dynamic, fallowing-based reserves could help landowners manage reduced groundwater availability while improving species' mobility in the face of climate change.

Introduction

Global environmental change is putting increasing pressure on agricultural production and on the natural resources that support and are affected by production, from groundwater to biodiversity (Norris, 2008; Tilman et al., 2011). Intensive agricultural production practices are driving severe soil degradation, disrupting biogeochemical cycles, and contributing to greenhouse gas emissions (Foley et al., 2005, 2011; Kopittke et al., 2019). Yet, the ecological and environmental costs of intensive production practices and global environmental change depend, in part, on the ecological and social context. Where high-value agriculture overlaps areas of high biodiversity there are difficult trade-offs between economic benefits, resources needed to support human population growth, and ecological conservation (Dudley & Alexander, 2017; Fischer et al., 2017; Larsen et al., 2020; Shackelford et al., 2015). Given that agriculture covers approximately 40% of ice-free land, understanding how to balance these inherent trade-offs is critical for the conservation of global biodiversity (Foley et al., 2005).

The immense influence of agriculture on biodiversity has necessarily spurred substantial ecological and conservation focus on how to manage agricultural landscapes to maintain both crop yields and biodiversity. Much of the debate thus far has centered on habitat. In other words, given a certain production is achieved, is it more beneficial for biodiversity to cultivate land intensively and set aside the remaining land for nature or is it better to cultivate a larger region with more wildlife friendly methods? This so-called land sparing/land sharing debate is sensitive to regional and focal taxa contexts. Though overly simplified here, research has generally illustrated that land sparing is most beneficial for disturbance sensitive species (Balmford et al., 2019; Feniuk et al., 2019; Phalan et al., 2011), while land sharing is most beneficial for agrobiodiversity (Kremen & Miles, 2012). Increasingly, the focus is not just on achieving current yields in more biodiversity-friendly ways, but rather on increasing yields to meet future demand, while maintaining, if not improving, biodiversity, ecosystem services, and social outcomes (Bommarco et al., 2013; Frei et al., 2020; Tscharntke et al., 2005). While the need for increasing yields with reduced environmental impacts is widely appreciated (Mockshell & Kamanda, 2018), the role of ecological versus technological approaches as well as the focus on biodiversity versus other social-ecological impacts (Rolf et al., 2019) remains a topic of debate.

Yet, agricultural land conversion and intensification do not just affect habitat availability and quality, but also the spatial matrix of different land uses (Bennett et al., 2006; Tscharntke et al., 2005). A landscape's spatial configuration, in turn, influences the movement of individuals and associated gene flow within and among populations, as well as dispersal and migration that may be critical to species' persistence (Doherty & Driscoll, 2018; Fahrig, 2007; Fraterrigo et al., 2009; Villard & Metzger, 2014). Particularly in intensive agricultural landscapes, connectivity between often rare and small patches of intact habitat may play key ecological functions (Baguette et al., 2013; Saura et al., 2014). However, creating such habitat connectivity corridors presents major challenges in working landscapes where available land is scarce.

Historically, conservation initiatives have focused on separating nature from areas of human economic activity and resource use through the use of protected areas (Folke, 2006). While protected areas remain the cornerstone of many conservation efforts (Maxwell et al., 2020), the importance of connectivity between protected areas, usually by way of fixed natural corridors through the landscape, is also well-established (Folke, 2006; Maxwell et al., 2020; Ward et al., 2020). However, both of these static conservation approaches are not always practical in (semi-) urban or high-value agricultural zones where setting aside land for conservation has high opportunity costs (Venter et al., 2018). Rather, more opportunistic and dynamic reserves–or adaptively managed protected areas with spatial distributions that change through time based on environmental impacts to biodiversity and agricultural production–may offer a feasible mechanism for provisioning habitat and enhancing connectivity in regions unlikely to be protected in perpetuity due to competing land-uses (Bengtsson et al., 2003; D'Aloia et al., 2019; Reynolds et al., 2017).

Dynamic reserves are increasingly appreciated as a means to enhance protected area networks to meet conservation goals (Bengtsson et al., 2003; D'Aloia et al., 2019). A substantial emphasis, to date, has been on aiding migrations. For example, in California, The Nature Conservancy paid farmers to create ephemeral wetlands on fallowed rice fields for migratory shorebirds, which resulted in increased shorebird density, richness, and diversity (Golet et al., 2018; Reynolds et al., 2017). Climate-driven migrations may also be supported by dynamic reserves. Many species migrating under changing climate conditions will encounter highly fragmented, human-dominated landscapes (Lawler et al., 2013). Particularly in areas with substantive competing human pressures and tradeoffs, reserves dynamically placed across the landscape to meet species' needs, while limiting opportunity costs incurred by local communities, will be crucial (Alagador et al., 2014; Hannah et al., 2007; Kattwinkel et al., 2011). Migratory species may not be the only species to benefit from dynamic reserves in human-dominated landscapes. For example, vagile species that utilize agricultural landscapes for dispersal, foraging, or other life history needs may also benefit from dynamic reserves which open new corridors through high-risk landscapes (Tucker et al., 2018; Zeller et al., 2020). In particular, the use of fallowing may serve as a dynamic conservation tool to support vagile species occupying intensive agricultural landscapes. In such a scenario, a network of agricultural land parcels would be set-aside and fallowed for a set time period to allow for increased landscape connectivity while also supporting potential co-benefits such as increased water table recharge, recovery of soil nutrients, and reduced pesticide and nutrient runoff (Bengtsson et al., 2003; D'Aloia et al., 2019; Golet et al., 2018; Raymond et al., 2017). While studies have explored the utility of dynamically fallowed lands as potential habitat, including in the high-value, intensively managed croplands of the San Joaquin Valley, CA (SJV) (Bryant et al., 2020;

Kelsey et al., 2018; Lortie et al., 2018; Stewart et al., 2019), few studies have focused on the potential habitat connectivity benefits stemming from fallowed lands (Lortie et al., 2018).

California, US, presents a valuable opportunity to understand the potential conservation benefits of dynamic reserves comprised of fallowed croplands. California is considered a biodiversity hotspot with ~1,500 plant and ~60 vertebrate endemic species across its 13 distinct level III ecoregions and is also home to some of the most valuable agricultural lands in the country, which underpin the economic and social fabric of many inland regions (Griffith et al., 2016; Harrison, 2013; Kelsey et al., 2018). The San Joaquin Valley is the agricultural powerhouse of California and is home to many endemic and endangered species which are greatly impacted by agricultural and urban development (Lortie et al., 2018; Stewart et al., 2019; U.S. Fish and Wildlife Service, 1998). From 2012 to 2016, California experienced its driest years on instrumental record, and the resultant water storage deficits led to billions in crop and livestock losses as well as a substantial increase in fallowed land in the San Joaquin Valley (Griffin & Anchukaitis, 2014; Medellín-Azuara et al., 2015, 2016). In response, the California legislature passed the Sustainable Groundwater Management Act (SGMA) in 2014. SGMA requires that by 2040 groundwater basins be managed such that they can provide a reliable water supply able to withstand future climate change induced drought conditions, while still providing multiple environmental and socioeconomic co-benefits (Roberts et al., 2021; California Water Code [CWC]. Division 6, Part 2.74. Sustainable Groundwater Management., 2014). As the majority of groundwater in California is withdrawn for agricultural uses, forecasts suggest that more than 300,000 ha of agricultural land in the San Joaquin Valley (~15% of irrigated cropland in the SJV) might need to be retired to achieve basin sustainability by the SGMA 2040 deadline (Bryant et al., 2020; Hanak et al., 2019). This potential policy-driven fallowing could provide considerable environmental and conservation co-benefits (Queiroz et al., 2014). In particular, fallowed lands, which we define here as land that does not produce a crop within a calendar year, could play a significant role as dynamic reserves in the San Joaquin Valley.

We focus on the potential of fallowed lands to facilitate habitat connectivity for the endangered and endemic San Joaquin kit fox (*Vulpes macrotis mutica*) (hereafter referred to as kit fox), since it is a vagile species, is disturbance sensitive, has well-studied historic distribution and ecology, is considered an umbrella species for regional fauna, and has designated high suitability core area in Kern county (Cypher et al., 2013; Haight et al., 2004; Koopman et al., 2000; U.S. Fish and Wildlife, 2020; U.S. Fish and Wildlife Service, 1998). Using a time series of fallowing scenarios, we examine how changes to fallowed areas in Kern County from 2011 to 2017 likely influenced potential functional connectivity between kit fox habitat areas. Beyond illustrating the connectivity benefits of fallowing for kit fox in this region, we discuss potential applications of these methods for future studies and collaborations around strategic fallowing and dynamic connectivity corridors.

Methods

Species & Regional Context

Our case study centers on habitat connectivity within Kern County, California, which is located in the southern San Joaquin Valley (Figure 1). Kern County is consistently one of the highest crop producing counties in California (California Department of Food and Agriculture, 2019). During the historic 2012–2016 drought, fallowed land within Kern potentially more than doubled (~45 kha in 2011 to ~93 kha in 2015 according to FAM data) due to low precipitation, high irrigation costs, and a patchwork of historical water rights (Gebremichael et al., 2021;

Medellín-Azuara et al., 2015, 2016). Climate-induced fallowing across the landscape makes Kern County a useful location to understand how such fallowing may influence species connectivity, which can provide valuable insight into potential biodiversity impacts of the Sustainable Groundwater Management Act (SGMA) and associated fallowing forecasts.

We focus on the San Joaquin kit fox to better understand the effect of drought-induced fallowing on endemic species' habitat and connectivity in Kern County. The kit fox was federally listed as an endangered species in 1967 and as threatened by the California Department of Fish and Wildlife in 1971 (U.S. Fish and Wildlife Service, 1998). Kit foxes are a vagile species that need high connectivity between core habitat areas for hunting and denning (U.S. Fish and Wildlife, 2020). They have home range sizes up to 24.1 km^2 and move between different dens after about 2-3 days (Cypher et al., 2019; U.S. Fish and Wildlife, 2020). Intensive agricultural and urban development throughout the SJV has resulted in severely fragmented habitat, disjointed kit fox populations, and high mortality rates (Cypher et al., 2013, 2019; U.S. Fish and Wildlife Service, 1998). Increased connectivity has been identified as key to avoiding local extinction and genetic bottlenecks in this species (U.S. Fish and Wildlife, 2020). Additionally, given its diverse habitat needs that encompass the habitat of many other locally endemic species, the kit fox has been identified as an umbrella species for upland taxa (U.S. Fish and Wildlife, 2020; U.S. Fish and Wildlife Service, 1998). As such, connectivity corridors for kit foxes have potential co-benefits, particularly for species that are also vagile, need high habitat connectivity for foraging and natal dispersal, and that alter their movement to areas with reduced stressors or risk of mortality.

Habitat suitability relationships for the kit fox have been identified from tracking studies, and these studies found that the most important habitat attributes for kit foxes are land use and cover, vegetation density, and terrain ruggedness (Cypher et al., 2013; Warrick & Cypher, 1998). Kit foxes have been documented to regularly use fallowed lands in addition to native grasslands and shrublands as they prefer low and sparse vegetation on flat or gently sloped lands, and have been observed to use these lands within weeks of fallowing, with use increasing as fields remain fallowed (Cypher et al., 2007; Warrick et al., 2007; White et al., 1995). Kit foxes avoid highly human-modified areas where possible—particularly urbanized and intensive, irrigated agricultural areas—as these landscapes can make it difficult and energetically costly for foxes to detect predators, capture prey, or avoid negative human interactions while on the move (Cypher et al., 2005, 2013; Cypher & Van Horn Job, 2012; Warrick et al., 2007; Warrick & Cypher, 1998; White et al., 1995). For example, while they have been shown to occasionally forage and travel through agricultural lands, intensive agricultural practices including irrigation, cultivation, pesticides, and harvesting as well as increased risk of predation from coyotes (*Canis latrans*) and non-native foxes (*Vulpes vulpes*) discourage kit foxes from crossing these lands and increase mortality risk for those that do cross (Cypher et al., 2005; Warrick et al., 2007).

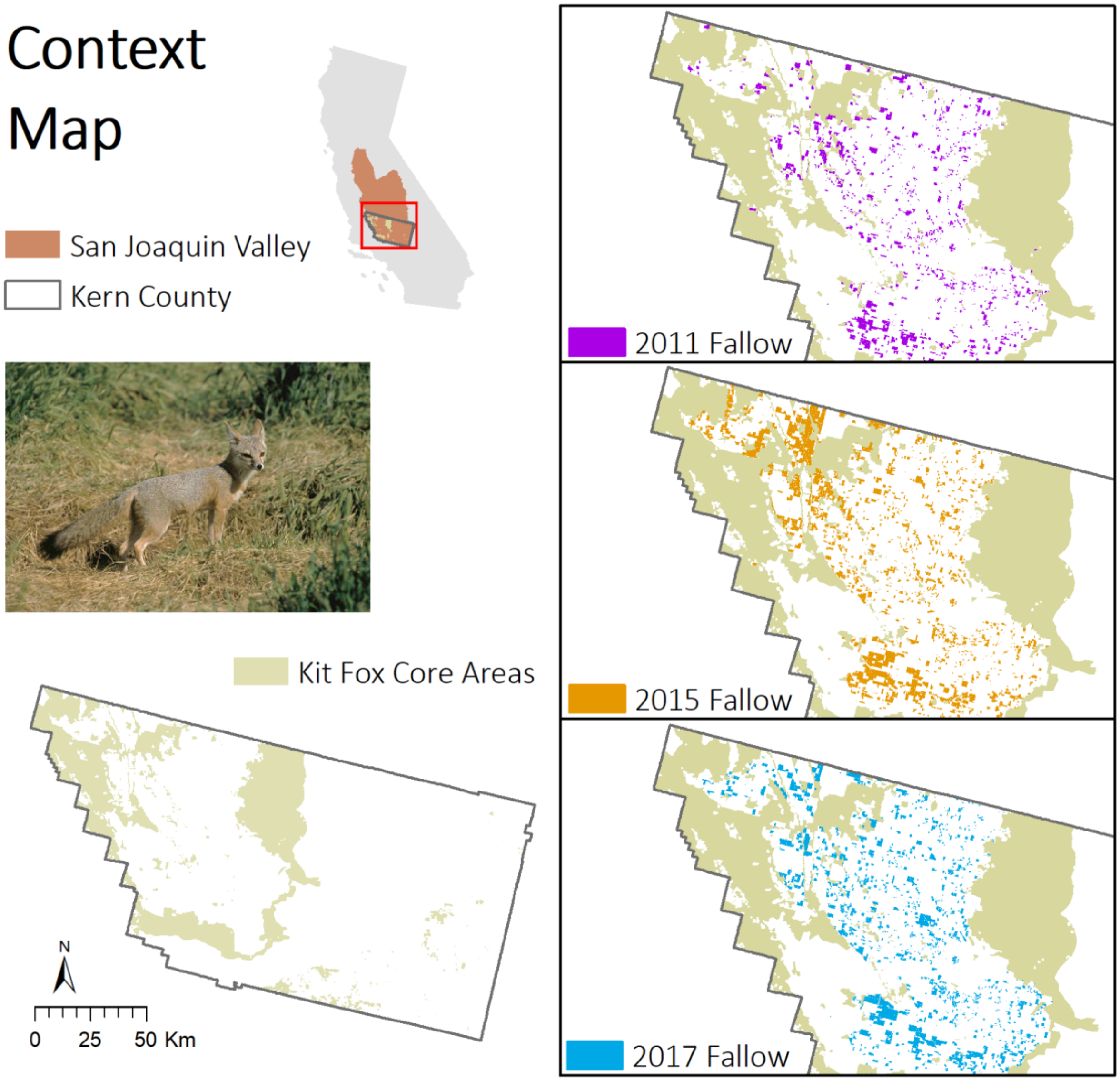

Figure 1. Context Map. Left panel, from top to bottom: San Joaquin Valley and Kern County context map, photo of Kit Fox, and high-value Kit Fox Core Areas within Kern County. Photo Credit: Peterson B Moose, U.S. Fish and Wildlife Service (Moose, 2021). Right panel: 2011 (~45 kha fallowed land), 2015 (~93 kha fallowed land), and 2017(~67 kha fallowed land) from Fallow Area Mapping (FAM) data (F. Melton, personal communication, 2020; Melton et al., 2015). All data layers described in text and Table S1.

Methodology Workflow

Modeling connectivity is, in essence, trying to capture how species move and what features of a landscape, be it anthropogenic (e.g., roads) or natural (e.g., vegetation type), facilitate or inhibit movement. Many connectivity modeling approaches are based on a resistance surface, which is a representation of the landscape features reflecting the difficulty with which an organism traverses, where difficulty reflects physiological costs and/or mortality risk (Diniz et al., 2020). We created resistance layers for the kit fox across the Kern County landscape derived from habitat suitability and barriers to movement layers. For rare and endangered species, many of which reside in agricultural landscapes like the kit fox, accurately modeling resistance is a challenge due to limited empirical observations of movement in addition to habitat occupancy. As such, many studies use a negative linear function or a negative exponential function (Diniz et al., 2020; Keeley et al., 2016, 2017; Trainor et al., 2013; Zeller et al., 2018) of habitat suitability to proxy resistance, which differ in how traversable low suitability habitat is assumed to be, and conduct sensitivity analyses on the development of the resistance surface. We took that approach here. We created multiple resistance layers per year to analyze the sensitivity of results to different assumptions of the energetic cost of movement for species to traverse across the landscape. We defined the core habitat areas of the San Joaquin kit fox and then ran spatial connectivity analyses to estimate how the spatial extent and distribution of fallowing affected landscape connectivity through its effect on landscape resistance. We statistically compared connectivity between the years of analysis, with 2011 as the base year of our analysis, 2015 as the year of the maximum extent and intensity of the drought in California, and 2017 as the final year of analysis, for all resistance sensitivity simulations. All processing and analyses were performed in R Statistical Software v3.5.3 (R Core Team, 2019) and ArcGIS 10.7.1. Figure 2 broadly depicts our approach to evaluating the effects of fallowing on kit fox habitat connectivity, with all data layers described in text below and Table S1.

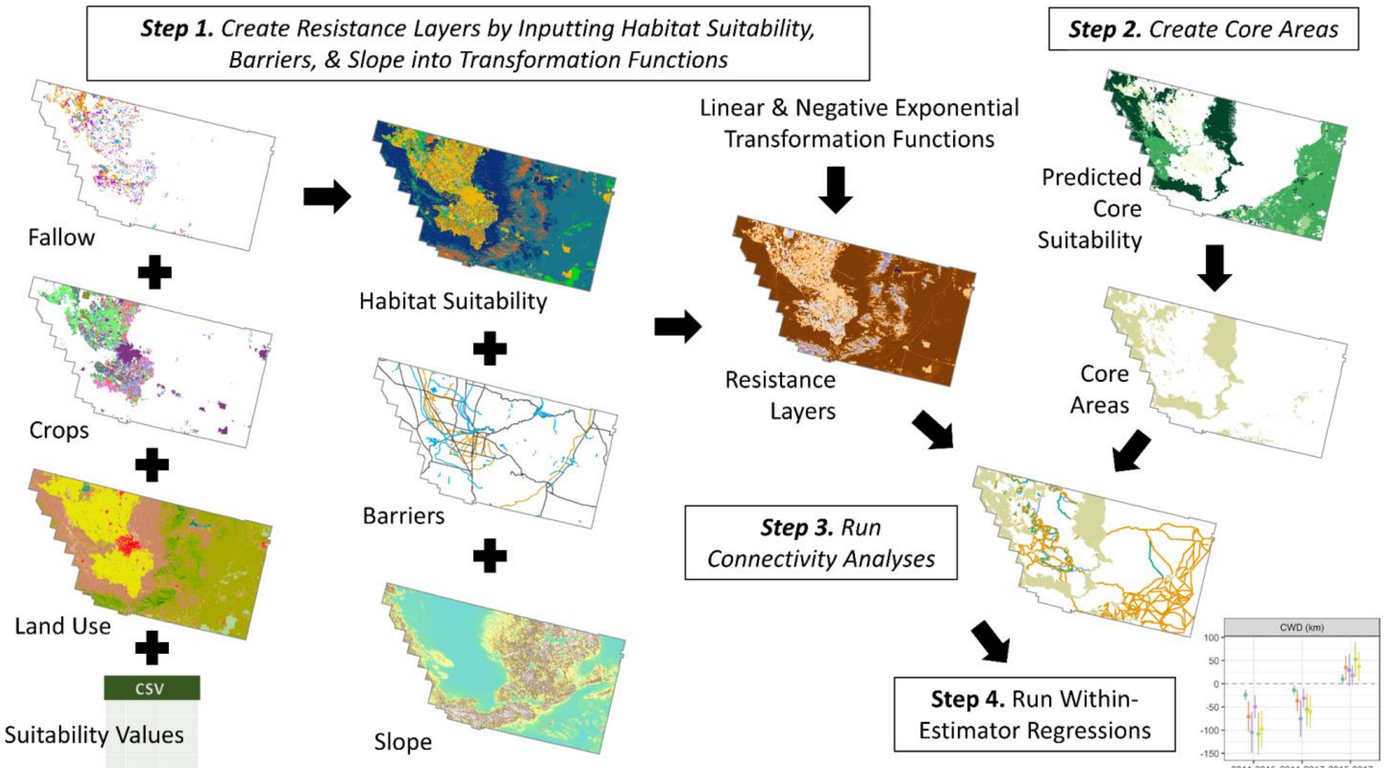

Figure 2. Methodology workflow diagram.

Resistance Layers

To analyze changes to kit fox mobility through Kern County, CA from 2011 to 2017, we created multiple resistance layers for each year of analysis, based on different sets of assumptions of kit foxes' sensitivity. Resistance surfaces reflect the "energetic cost, difficulty, or mortality risk" (McRae & Kavanagh, 2011, 2017) for the species to move across each cell. To create resistance surfaces that best reflect the continuous gradient of energetic costs incurred by kit foxes, we incorporated habitat suitability (defined by land covers), slope angle, and stressors to kit fox movement, as described below (SI Methods for additional information).

We transformed land cover maps into habitat suitability using suitability values compiled across previous studies of kit fox habitat use (Cypher et al., 2013)(Table S2). Many of these earlier studies tracked actual kit fox habitat use and movement through radio-collars, scat, and other methods (Cypher et al., 2000; Warrick et al., 2007; Warrick & Cypher, 1998; White et al., 1995), and have been used in other studies of kit fox movement (Nogeire-McRae et al., 2019).

Land cover was defined from three land use datasets: annual, satellite-derived fallowed area data layers (30m rasters) for 2011 to 2017 from the NASA-USGS-USDA Fallowed Area Mapping (FAM) project (Boryan et al., 2011; Medellín-Azuara et al., 2015; F. Melton, personal communication, 2020; Melton et al., 2015), statewide crop mapping shapefiles from Land IQ LLC and California Department of Water Resources (DWR) for 2014 and 2016 (California Department of Water Resources, 2017, 2019), and aggregate land cover layers (30m rasters) of 2011 and 2016 from the USGS National Land Cover Database (NLCD) (Jin et al., 2019). The annual FAM datasets were used to locate fallowed areas for these analyses, where 'fallowed' is defined as land that did not produce a crop within a calendar year. Non-irrigated lands exhibiting volunteer crop growth or evidence of a non-irrigated winter cover crop in January–February or November–December were considered fallow. According to the FAM data, fallowed cropland in Kern increased from ~45 kha in 2011 to ~93 kha in 2015, before decreasing to ~67 kha in 2017. The FAM provides plausible scenarios of the extent of fallowing during a multi-year drought. We build on that to understand how connectivity can potentially respond to such large-scale changes in land use.

After harmonizing the extent and spatial resolution of the three land use datasets, we combined them into one consolidated land cover map for Kern County. As we wanted to evaluate how the change in fallow area—defined as a binary variable based on the annual FAM data—influenced the change in species connectivity across the years, we combined the FAM input in each year of analysis from 2011 to 2017 with the 2016 DWR dataset and the 2016 NLCD (Figure 1). We later examined the impact of these static layers by comparing the connectivity results from the 2011 FAM data combined with the 2016 DWR and 2016 NLCD data to the results from the 2011 FAM data combined with the 2014 DWR and 2011 NLCD data. To combine the layers together we gave precedence to FAM, then DWR, and then NLCD.

Since the difficulty of traversing fallowed land may differ based on the duration of fallowing (Cypher et al., 2007), we evaluate two different suitability scenarios. First, we consider the suitability of all fallowed lands as "retired", or fallowed for more than one year, to mimic what we might expect in a drought or under SGMA, in which fallow lands are assumed to more closely resemble grassland or shrubland due to a longer duration of fallowing and therefore increased vegetative recovery and habitat suitability in these semi-permanent areas (Cypher et al., 2007, 2013). Second, we evaluated fallowed lands as "idle", or fallowed for one year, in which they are assumed to more closely resemble barren land due to the shorter-term and more transitory nature of fallowing (Cypher et al., 2013). As the distribution of fallowed lands from 2011 to 2017 was likely a combination of these land types, we chose to evaluate these two suitability scenarios to bound our results. Results associated with these two types of fallow land are hereafter referred to as 'retired' and 'idle' results, respectively.

To capture stressors to movement, we also included the presence of roads, rivers, and agricultural canals, all of which can increase the cost and risk of movement for kit foxes across the landscape. For roads (U.S. Census Bureau, 2019), we gave primary roads the lowest value of suitability (0), since urban roads and vehicle collisions have been shown to be a major cause of mortality in studies of dispersing kit foxes; secondary roads were given slightly higher values (0.1) as less detrimental (Bjurlin et al., 2005; Cypher & Van Horn Job, 2012). We include rivers (Buto & Anderson, 2020; United States Geological Survey (USGS), 2020) as well as agricultural canals (Department of Water Resources, 2021) in our resistance layers, also given a low suitability value of 0, again based on the likely higher risk and stress cost for foxes to pass these features (Cypher et al., 2005, 2013; McRae et al., 2016). Lastly, we calculated percent slope, using 30m elevation raster files from the National Elevation Dataset (Gesch et al., 2018; United States Geological Survey (USGS), 2018), as kit fox prefer flat or gently sloping areas (Cypher et al., 2013; Warrick & Cypher, 1998).

Though empirical data on kit fox habitat use exists, empirical data on barriers to dispersal for a representative population is not available. We therefore evaluate the sensitivity of our results to different resistance representations through different transformation functions—a negative linear transformation and a negative nonlinear exponential transformation—of habitat suitability to resistance (Diniz et al., 2020; Keeley et al., 2016, 2017; Trainor et al., 2013). With the negative linear transformation, resistance is the inverse of suitability, which assumes that areas of higher suitability offer low resistance to movement (Keeley et al., 2016, 2017). We apply three different negative linear transformations, using equations outlined in Dickson et al. (2017):

$$\textit{Linear Eq. 1:}\ R_1 = 1 + \left(H^{(0.8-s)^2}\right) \times 1000$$

$$\textit{Linear Eq. 3:}\ R_3 = 1 + (1000 \times H^2) + \frac{s}{4}$$

$$\textit{Linear Eq. 5:}\ R_5 = (H + 1)^{10} + \frac{s}{4}$$

where H is the maximum resistance value across combined human modification layers (land use, stressors) and s is percent slope (Dickson et al., 2017).

Moving from Linear Eq. 1 to Eq. 5 assumes an increasing sensitivity to human modification, and Dickson et al. 2017 selected Eq.5 as the final model as it had the most reasonable and least exaggerated resistance values for land covers with low human modification (Dickson et al., 2017; Lawler et al., 2013).

Recent studies indicate that a negative exponential relationship between habitat suitability and resistance may be a more accurate representation of species movement during dispersal and mating (Diniz et al., 2020; Keeley et al., 2016, 2017; Trainor et al., 2013; Zeller et al., 2018). For the vagile kit fox, which is known to traverse agricultural and urban lands while hunting, mating, and searching for den sites even though it incurs a higher risk and energetic cost, such a representation is warranted. To create resistance surfaces using a negative exponential function, we used the transformation function presented in Trainor et al. 2013 and Keeley et al. 2017, scaled by 10:

Negative Exponential c 0.25, c 4, c 8: $R = (100 - 99 \times \left(\frac{1-exp(-c \times h)}{1-exp(-c)}\right)) \times 10$

where c defines the nonlinear relationship between habitat suitability (h) and resistance (R) (Keeley et al., 2017; Trainor et al., 2013). We scaled R values by a factor of 10 as connectivity analysis software prefers larger values for computations, and to match the relative scale of the Dickson equations. To assess the sensitivity of our results to the shape of the exponential relationship between habitat quality and resistance values, we used three different values of c (0.25, 4, and 8), hereafter referred to as the Negative Exponential c 0.25, c 4, and c 8 equations, where c=0.25 represents a nearly linear relationship (Keeley et al., 2017). Additionally, we assessed the sensitivity of our results to the two duration of fallowing suitability scenarios—longer term, semi-permanent retired versus shorter term, temporarily idle fallowed lands. All combinations of years (n=3), resistance equations (n=6), and types of fallow land (n = 2) resulted in 36 unique resistance layers. For each of these resistance representations, the computed 30 m resistance surface layers (for each year) were aggregated to 270-meter resolution for input into spatial connectivity analysis software.

Kit Fox Core Areas

We identified critical kit fox habitat using the California Wildlife Habitat Relationships (CWHR) Predicted Habitat Suitability raster (30m) (California Department of Fish and Wildlife California Interagency Wildlife Task Group, 2016), which ranks habitat quality for core areas using a mean habitat suitability score (0 to 1 for low to high quality, respectively). Habitat suitability scores for kit fox are based on the average value of expert defined reproduction, cover, and feeding scores for the species in the habitat type, and areas of high quality are where the likelihood of habitat needs being met is high. We created habitat area polygons by aggregating the 30 m CWHR habitat suitability raster to 270 meters around the median scores, and then defined core habitat areas as polygons greater than 5 ha with the highest suitability scores (SI Methods), as large, high suitability areas represent likely sources of dispersing individuals (Diniz et al., 2020).

Spatial Connectivity Analyses

To examine how changes in fallowed areas likely impacted kit fox movement through the Kern County landscape we used Circuitscape and least-cost path approaches (McRae, 2013; McRae & Kavanagh, 2011, 2017; McRae & Shah, 2009). Both approaches model movement of an organism between core areas based on the resistance landscape. We chose these approaches rather than individual based modeling approaches due to our focus on understanding how a change in land use affects landscape connectivity over a broad spatial scale and due to a lack of available dispersal parameters. Circuitscape relies on circuit theory to model probabilistic species movement through the landscape as a function of current flow (McRae et al., 2008; McRae & Shah, 2009). Circuitscape models movement as a resistance-weighted random walk between two core areas, where, in our case, an individual perceives and responds to the landscape in the 270m pixels nearby. In contrast, the Least-Cost Path Length (LCP) identifies the single pixel wide least-cost path an assumed to be omniscient individual would take, or the pathway with the lowest cumulative cost of movement (McRae et al., 2012; McRae & Kavanagh, 2017). Both tools can be combined such that Circuitscape is run through "least-cost" corridors spanning the least cost path to identify potential bottlenecks to species movements, or pinch points, using the Linkage Mapper toolbox (McRae et al., 2012; McRae & Kavanagh, 2011, 2017). We truncated corridors at a width of 200 cost-weighted km and dropped corridors that intersected core areas, as we were interested in the change in movement between, and not through, core areas. For our analyses, we used Circuitscape 4.0 (McRae, 2013) and Linkage Mapper 2.0 (McRae & Kavanagh, 2011) through the ArcGIS Toolbox (SI Methods).

Statistical Analyses

We performed statistical comparisons of our spatial connectivity analyses to examine changes in potential functional habitat connectivity as fallow area changed from 2011 (start of drought) to 2015 (peak) to 2017 (drought subsides). We focused on measures of Cost-Weighted Distance (CWD), Least Cost Path (LCP) Length, Cost Weighted Distance to Least Cost Path Length Ratio (CWD:LCP), and Effective Resistance (ER) for our least cost paths. CWD for least-cost paths is the amount of resistance accumulated by an individual when moving optimally between core areas, and is estimated in units of cost-weighted meters (McRae et al., 2012). We used the metric CWD:LCP, which is a ratio of the CWD to the physical distance of the least cost path, as well as examining the CWD and LCP Length metrics that compose it, both of which we have converted to km. When comparing CWD:LCP values within a given study, higher values indicate paths that are more costly to individuals. ER, often referred to as resistance distance, is a measure of isolation between a pair of core areas, as it accounts for multiple pathways, and is in units of Ohms (McRae et al., 2008; McRae & Shah, 2009). We used a within-estimator model predicting CWD, LCP Length, CWD:LCP, and ER as a function of year dummy variables absorbing core-to-core identifiers and clustering the standard errors at the same level (Larsen et al., 2019; Wooldridge, 2010). We ran within-estimator regressions for connectivity output associated with each of the resistance surfaces described above to assess the sensitivity of connectivity model outputs to changes in resistance assumptions.

Results

Resistance Models

For each of the three years of analysis (2011, 2015, 2017), six resistance models were developed (3 linear and 3 negative exponential) for both fallow lands defined as retired and idle farmland, resulting in 36 resistance layers in total. There were stark visual differences between resistance models in levels of energetic cost across the landscape, reflecting the degree of permissivity to movement in the model structure (Figure 3). For example, Linear Eq. 1 and Negative Exponential c 0.25 had higher resistance penalties for less suitable areas, and so had greater resistance cost values across the landscape than more permissive models such as Linear Eq. 5

and Negative Exponential c 8 (Figure 3). Still, a Pearson correlation between all of the resistance models for each individual year revealed that the different models were overall highly correlated (>0.7) with most, besides Linear Eq. 1, having correlation coefficients above 0.9 (Table 1; Table S3).

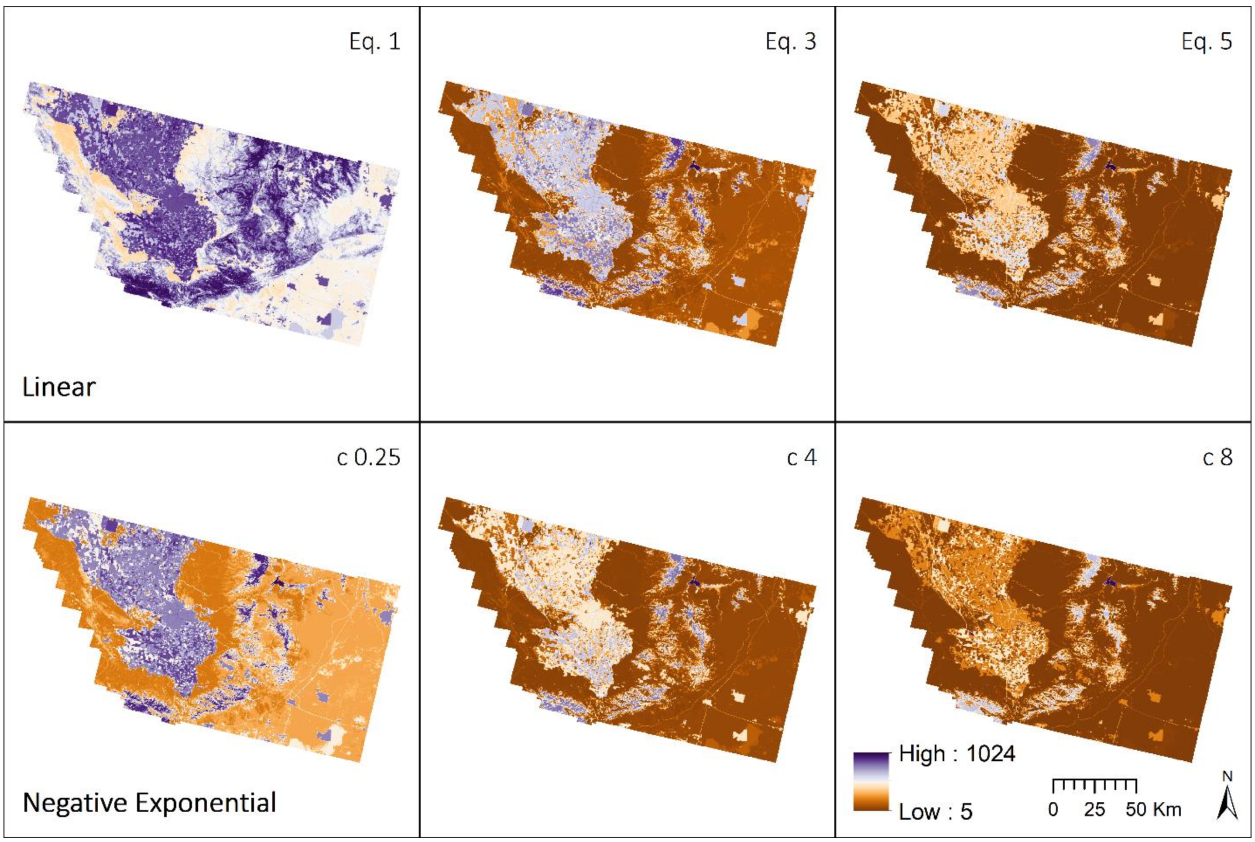

Figure 3. Resistance layers for all 6 resistance models for 2011 for fallow defined as idle farmland, all scaled to 5–1024 resistance range (Ohms). Permittivity increases left to right, with the two rows reflecting different transformations of habitat suitability to resistance (see methods). Purple coloration indicates areas of high resistance. Resistance layers for retired fallow land were similar, with only fallow parcels as lower resistance scores.

Table 1. Pearson correlation values between all 6 resistance models for 2011 for fallow defined as idle farmland.

	Eq. 1	Eq. 3	Eq. 5	c 0.25	c 4	c 8
Linear Eq. 1	1					
Linear Eq. 3	0.74	1				
Linear Eq. 5	0.73	0.97	1			
Negative Exponential c 0.25	0.73	0.99	0.94	1		
Negative Exponential c 4	0.74	0.99	1.00	0.97	1	
Negative Exponential c 8	0.70	0.92	0.98	0.88	0.97	1

Least Cost Path Summaries

Least Cost Path summaries across all models are available in Table S4. The Cost Weighted Distance (CWD) to Least Cost Path (LCP) Length Ratio (CWD:LCP), or the cost of movement encountered by an individual per km traveled on the least cost pathway, was highest in 2011, at the onset of the drought, and was lowest in 2015, at the height of the drought, reflecting the increasing potential availability of fallowed lands. Model outputs varied in their absolute CWD:LCP values, as expected, though the patterns between years and between fallow land definitions were fairly consistent (Table S4). Negative Exponential c 8 (most permissive) always had the lowest average CWD:LCP values, while Linear Eq. 1 (least permissive) was often an order of magnitude higher. For the most permissive model, there was a ~8.9% decrease in average CWD:LCP from 2011 to 2015 for idle farmland models and ~14.3% decrease for retired farmland models. Additionally, there was a ~4.0% (idle) to 7.9% (retired) decrease from 2011 to

2017 and a ~5.4% (idle) to 7.4% (retired) increase from 2015 to 2017. Conversely, the Least Cost Path Length (km), or the distance an individual travels following the least cost path from one core area to another, showed the opposite trend. Thus, while the paths became slightly longer in 2015 and 2017 relative to 2011 in terms of LCP Length (increase in mean value from 2011 to 2015 by ~0.6 to 4.0% across idle models and ~1.5 to 6% across retired models, and from 2011 to 2017 by ~0.8 to 4.6% for idle models and ~1.0 to 5.3% for retired models), they were less costly and there was a lower resistance to individuals. For most models, changes in CWD across years were more influential in driving changes in CWD:LCP than changes in LCP length, although this relationship was more prominent in model outputs associated with retired farmland than idle farmland (Table S4). Effective Resistance (Ohms) metrics were more model dependent. However, these summarized metrics were averaged across all pathways, and do not account for the paired nature of pathways, or changes in movement between the same core areas. Thus, while these summaries illustrate overall trends in mobility across the landscape, they do not account for the paired nature of pathways between any given core areas.

Paired Core Analysis

For our within-estimator models, which evaluate differences in core-to-core connectivity metrics, we saw similar patterns between years across resistance models (Figure 4; Table S5). The average CWD:LCP, which measures movement costs accumulated per km traveled on the LCP, was significantly ($p<0.01$) lower in 2015 relative to 2011 (-7.54 ± 1.90 to -28.08 ± 5.49 (+/-SE) for retired and -5.24 ± 1.92 to -10.92 ± 3.52 (+/-SE) for idle) across all models (Table S5), which corresponded to roughly a 4 to 18% decrease in CWD:LCP for retired farmland models and a 0.8 to 9.8% decrease for idle farmland models relative to the average values across all LCP in 2011 (computed from Table S4 and S5). CWD:LCP was also significantly reduced in 2017 relative to 2011 for all retired models ($p<0.01$) and some idle models ($p<0.05$), but to a lesser degree for both retired (-5.07 ± 1.64 to -19.27 ± 4.94 (+/-SE)) and idle (-2.11 ± 1.62 to -6.06 ± 3.31 (+/-SE))(2.6 to 12.2% relative decrease for retired and 0.3 to 6.0% relative decrease for idle) (Table S5). The differences in CWD:LCP between 2015 and 2017 were not significant for most models, though were consistently positive, as expected (Table S5; Figure 4). Comparing retired versus idle models for scenarios in which fallowing increased according to the FAM (2011 to 2015/2017), reductions in CWD:LCP were more than 3 times greater on average for the retired models (representing longer term fallowing) than the idle models (shorter term fallowing).

CWD (accumulated cost) showed similarly significant decreases in 2015 ($p<0.01$) and 2017 ($p<0.05$) relative to 2011 for most models (~2.3 to 12.8% and 1.4 to 8% decrease for 2015 and 2017, respectively, relative to 2011 averages for retired farmland, and ~0.7 to 7.7% and 0.4 to 3.6% decrease for 2015 and 2017, respectively, relative to 2011 averages for idle farmland) (Table S5). Model results also showed increases in CWD from 2015 to 2017 (0.9 to 5.6% increase relative to 2015 averages for retired farmland models, and 0.3 to 4.0% increase relative to 2015 averages for idle farmland models), four of which were statistically significant ($p<0.05$) for both idle and retired models (Linear Eq. 1 and Eq. 3, Negative Exponential c 4 and c8) (Table S5). Similar to CWD:LCP, comparing retired versus idle models under scenarios of fallowing increase, reductions in CWD for retired models on average were more than double that of idle models.

Changes in LCP Length and Effective Resistance were fairly consistent across most models, but the results were less frequently significant (Figure 4; Table S5). For LCP Length, only Linear Eq. 3 from 2011 to 2015 for retired farmland was significant ($p<0.05$) with an increase of 0.1 ± 0.05 (+/-SE) (~1.2% increase relative to 2011 average), with most path lengths marginally increasing (2011 to 2015/2017) or remaining relatively consistent (2015 to 2017) between years (Table S5). These nonsignificant changes in LCP lengths and the statistically significant changes in CWD indicate that changes in CWD drove the responses seen in CWD:LCP (Table S5). For Effective Resistance, all models except the most restrictive (Linear Eq. 1), showed a significant ($p<0.05$) decrease between 2011 to 2015 for retired models (5.4 to 12.1% decrease relative to 2011 average for significant models); idle followed a similar but more muted trend with only the most permissive Negative Exponential c 8 model being significant ($p<0.05$) (Table S5). Effective Resistance from 2011 to 2017 showed reductions across most scenarios, but results for most models were not statistically significant (Figure 4; Table S5). For LCP length, increases in path lengths under scenarios of increased fallowing were on average more than double for retired models versus idle models. Between 2011 to 2015, reductions in ER for retired models were on average about double that of idle models, while patterns between 2011 to 2017 were less consistent. Averaging across all metrics for scenarios examining an increase in fallowing, values were on average 2.4 times greater with longer term, retired fallowing than shorter term, idle fallowing. Overall, trends highlighted that connectivity metrics improved significantly in 2015 relative to 2011 and remained elevated even when the drought broke in 2017, particularly the longer the land potentially remained fallowed.

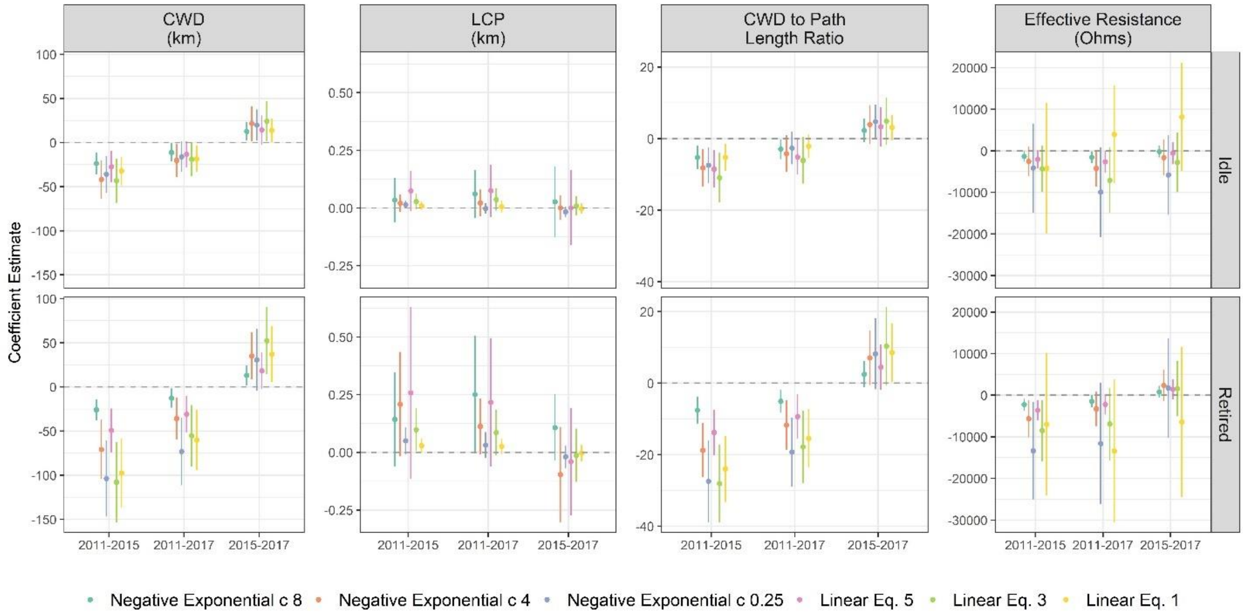

Figure 4. Within-estimator regression results for each resistance model between comparison years for fallow land defined as shorter term, idle farmland (top row) and longer term, retired farmland (bottom row).

Discussion

Climate change is likely to increase transitory and/or semi-permanent fallowing of farmland as drought, ground water limitations, and other unfavorable conditions become increasingly frequent and severe. Here we sought to understand how landscape changes driven by drought-induced fallowing in Kern County, California, US potentially impacted functional landscape connectivity for the endangered San Joaquin kit fox, a species of great conservation concern in the region (U.S. Fish and Wildlife, 2020; U.S. Fish and Wildlife Service, 1998). Across numerous models, our results suggest that habitat connectivity for San Joaquin kit fox likely increased from 2011 to 2015 as drought severity and the extent of fallowed farmland increased, then slightly decreased with drought severity and fallowing in 2017. These results were driven by an estimated decrease in the difficulty of traversing between high quality habitat areas, on average, despite an increase in the length of the best or “least cost” path.

Connectivity improvements manifest as a reduction in the difficulty of traversing between two high quality patches or core areas. Increases in potential functional connectivity from 2011 to 2015/2017 were apparent in statistically significant ($p<0.05$ to $p<0.001$) reductions in average Cost-Weighted Distances between core habitat areas across most models (~0.7 to 12.8% and 0.4 to 8% decrease relative to beginning of the drought averages, for 2015 and 2017 respectively, across retired and idle farmland models), and Effective Resistance showed similar though less significant trends between paired pathways. Additionally, despite least cost path lengths increasing from 2011 to 2015/2017, Cost Weighted Distance to Least Cost Path Length Ratios (CWD:LCP) decreased in those timeframes (~0.8 to 18% and 0.3 to 12.2% relative decrease during the drought, for 2015 and 2017 respectively, across retired and idle models), indicating that cumulative costs incurred by kit foxes traveling along LCPs may have decreased. The increased length of LCPs is a consequence of the patchwork of reduced-resistance, fallowed parcels that yielded a more circuitous, if lower resistance, path, on average.

Fallowed as a land type represents different land covers and land uses. Idle farmland models, which treat fallowing as highly transitory and similar to barren lands, showed muted responses in comparison to retired farmland models, which model fallowing as a more persistent land cover similar to grassland and shrubland; however, metrics associated with changes in cost weighted distance, particularly for 2011 to 2015 results, remained significant and patterns were fairly consistent across idle and retired models. The extent and distribution of drought-induced fallowing across Kern County, CA from 2011 to 2017 was likely a combination of these idle and retired farmland scenarios, as we would expect in other regions during and outside of droughts.

Thus, our models attempt to capture the upper and lower bound of landscape connectivity scenarios experienced by San Joaquin kit foxes throughout the 2011 to 2017 timeframe. Broadly, these findings highlight that fallowed parcels may provide important conservation value by increasing functional landscape connectivity through intensive agricultural landscapes, whether fallowed short- or long-term. However, under scenarios of increased fallowing, the benefits were on average 2.4 times greater with longer term fallowing.

Kit foxes disperse in response to biological pressures—a risky process involved with increased energy, predation, and competition costs—and thus are more likely to take advantage of even ephemeral changes in suitability (Cypher et al., 2019; Koopman et al., 2000). Small improvements to connectivity in an otherwise intensive agricultural landscape could significantly impact recovery for the federally listed species, as kit foxes make use of recently fallowed fields for both diurnal and nocturnal activities (Kelsey et al., 2018; Stewart et al., 2019; U.S. Fish and Wildlife Service, 1998; White et al., 1995). Indeed, according to FAM data, we saw fallowing double in the region from 45 kha in 2011 to 93 kha in 2015, with models suggesting that kit foxes likely experienced more permissive travel across Kern County in 2015 relative to 2011, and also had more paths connecting core habitat areas with relatively lower energetic cost and mortality risk. Particularly in Kern County, with contiguous high-intensity cropland between kit fox core areas, kit foxes may not be able to cross without intermittent refugia throughout. Connectivity is increasingly important in areas of lower habitat productivity and contiguity such as Kern County, as kit foxes increase space use and movement to find prey as a result of lower food availability in these less productive and suitable areas (White & Garrott, 1999; White & Ralls, 1993). Increased facilitation across these lands is especially important during drought years, as kit foxes suffer episodic declines during multi-year periods of drought from reduced prey availability and water limitations, which exacerbate local extinction and genetic bottleneck effects (Cypher et al., 2000; White & Garrott, 1999; White & Ralls, 1993). Given the potential increase in fallowing under the Sustainable Groundwater Management Act, which is estimated to reach about 300,000 ha across the SJV, and the increasing need for species' mobility in response to climate changes and drought, such increases in connectivity present a promising conservation opportunity.

Conservation lands are often heavily skewed towards high elevation and poor soil areas (Aycrigg et al., 2013). The opportunity costs of developing permanent reserves or movement corridors in productive agricultural landscapes are high and far-reaching (Bourque et al., 2019) and cultural ties to farming often extend generations (Kelsey et al., 2018), making large-scale static conservation corridors in working landscapes largely implausible. Thus, habitat conservation in predominantly agricultural or working landscapes may require opportunistic strategies for increasing landscape connectivity, such as the use of dynamic corridors between established protected areas (Bengtsson et al., 2003). More specifically, reserves that take advantage of transitory and semi-permanent land use changes, such as short- and long-term fallowed farmland, may be a viable solution for increasing habitat connectivity in areas of high economic and ecological value (Ando & Hannah, 2011; Moilanen et al., 2014). Dynamic corridors could also be more adaptive to extreme climate shocks, which is increasingly vital under compounding anthropogenic and climate stressors (D'Aloia et al., 2019; Larsen & McComb, 2021; Zeller et al., 2020).

While our analysis focused on drought-induced fallowing as an opportunistic source of increased connectivity for kit foxes, more strategic and collaborative fallowing could likely provide even greater benefits by purposefully setting aside lands based on biodiversity value and landscape context. Such collaborations could be incentivized through agri-environmental programs that pay farmers to temporarily or (semi-)permanently fallow particular fields. Broadly speaking, agri-environmental schemes for biodiversity conservation have been used successfully across the US and globally, including direct payments and subsidies to farmers who adopt environmentally beneficial practices and fallowing rotations (Bourque et al., 2019; Kuussaari et al., 2011; Ribaudo et al., 2010; Sanz- Pérez et al., 2019; Tarjuelo et al., 2020; Toivonen et al., 2013). In California, conservation payments could tap into available funding mechanisms and environmental initiatives, such as USDA funded conservation initiatives, Sustainable Groundwater Planning Grant Program funding for projects that increase sustainable groundwater, and state funding from California's newly established Biodiversity Collaborative (Bourque et al., 2019; California Department of Water Resources, 2021; Office of Governor Gavin Newsom, 2020). Additionally, these agri-environmental schemes could account for the numerous co-benefits of fallowing when allocating funding, including improved soil quality, increased water storage, and increased yields post-fallowing (Bourque et al., 2019; Kremen & Miles, 2012; Oliver et al., 2010). To derive the requisite benefits from tax payer funded agri-environmental schemes necessitates a thorough understanding of the socio-ecological system.

Our study adds to understanding of how dynamic reserves of fallowed lands may function to improve connectivity in working landscapes, yet has several limitations of note. First, our case study focuses on one species in one agriculturally-dominated county. Kit fox are highly vagile and may not represent the movement capability of less mobile species of concern such as the endangered kangaroo rats and blunt-nose leopard lizard (U.S. Fish and Wildlife, 2020; U.S. Fish and Wildlife Service, 1998). However, we generally expect less vagile species to be more sensitive to reductions in agricultural disturbances; additionally, less vagile species may be less likely to traverse an agricultural landscape in general, and approaches within already protected areas may be the most beneficial. Second, as with most connectivity modeling efforts (Diniz et al., 2020), we lack empirical data on species movement to validate our connectivity models, and like many other studies we rely on information about habitat suitability and findings from other studies, some of which contain movement data. While we include sensitivity analyses around the resistance layers, all are based, in part, on habitat suitability rather than dispersal suitability. Collecting species movement data with specific regards to fallowed lands would be extremely valuable to understand how factors such as seasonality, time, and individual variability influence dispersal and, of course, to validate connectivity modeling efforts such as ours. Further, research targeting the ecological memory, site fidelity, and gene flow of San Joaquin kit foxes, or other species of interest, would be crucial to determining the ecological and evolutionary value of increased connectivity and to ensure corridors do not introduce any perverse or deleterious outcomes (Larrosa et al., 2016).

Dynamic conservation actions have the potential to reduce the conflict between biodiversity preservation and agricultural production in agricultural landscapes. Here we show that estimated increases in fallowing from 2011 to 2015/2017 in Kern County likely increased functional landscape connectivity for the San Joaquin kit fox, with decreases in the relative cumulative cost incurred over distance traveled ranging from ~0.8 to 18% and 0.3 to 12.2% (2015/2017), with potential benefits across metrics, on average, 2.4 times greater with more suitable, longer-term fallowed lands. These results illustrate the potential for co-benefits to be derived amidst significant land use changes associated with drought conditions and the impending implementation of SGMA. Though the opportunity costs of fallowing to farmers under SGMA will likely be high, those costs have the potential to be partially offset by tapping into the conservation potential of dynamic reserves and conservation corridors comprised of either temporarily and/or semi-permanent fallowed lands. Given the ubiquity and influence of productive landscapes on human and natural systems and the increasing preponderance of uncultivated land therein, strategic and coordinated fallowing paired with dynamic and opportunistic conservation may be key to biodiversity conservation in agricultural landscapes.

Declarations

Funding

SM was supported in part by the Four-Year Fellowship program at the University of British Columbia, Vancouver. CP was supported in part by the Interdisciplinary Quantitative Biology (IQ Biology) Ph.D. program at the BioFrontiers Institute, University of Colorado Boulder. AEL acknowledges support from the US National Science Foundation (No. 2042526) and the US Department of Agriculture (No. 2022-67019-36397).

Conflicts of interest

We declare no conflicts of interest.

Ethics approval

No ethics approvals were required for conducting this study.

Consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

FAM data will be available upon request from Forrest Melton. All other data is publicly downloadable from the sources cited, and processed in the manner described in the Methods and SI Methods.

Code availability

Code is available upon request from reviewers.

Authors' contributions

Sofie McComb and Ashley Larsen conceptualized and designed the study. Material preparation and data collection were performed by Sofie McComb, and supported by Forrest Melton with regards to supplying Fallow Area Mapping data. Sofie McComb, Ashely Larsen, and Claire Powers performed the formal analysis and investigation, and contributed to the first draft of the manuscript. All authors reviewed and edited previous versions of the manuscript, and read and approved the final manuscript.

References

Alagador, D., Cerdeira, J. O., & Araújo, M. B. (2014). Shifting protected areas: Scheduling spatial priorities under climate change. *Journal of Applied Ecology*, *51*(3), 703–713. https://doi.org/10.1111/1365-2664.12230

Ando, A. W., & Hannah, L. (2011). Lessons from finance for new land-conservation strategies given climate-change uncertainty. *Conservation Biology*, *25*(2), 412–414.

Aycrigg, J. L., Davidson, A., Svancara, L. K., Gergely, K. J., McKerrow, A., & Scott, J. M. (2013). Representation of Ecological Systems within the Protected Areas Network of the Continental United States. *PLoS ONE*, *8*(1), e54689. https://doi.org/10.1371/journal.pone.0054689

Baguette, M., Blanchet, S., Legrand, D., Stevens, V. M., & Turlure, C. (2013). Individual dispersal, landscape connectivity and ecological networks. *Biological Reviews*, *88*(2), 310–326.

Balmford, B., Green, R. E., Onial, M., Phalan, B., & Balmford, A. (2019). How imperfect can land sparing be before land sharing is more favourable for wild species? *Journal of Applied Ecology*, *56*(1), 73–84. https://doi.org/10.1111/1365-2664.13282

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Folke, C., Ihse, M., Moberg, F., & Nyström, M. (2003). Reserves, Resilience and Dynamic Landscapes. *AMBIO: A Journal of the Human Environment*, *32*(6), 389–396. https://doi.org/10.1579/0044-7447-32.6.389

Bennett, A. F., Radford, J. Q., & Haslem, A. (2006). Properties of land mosaics: Implications for nature conservation in agricultural environments. *Biological Conservation*, *133*(2), 250–264.

Bjurlin, C. D., Cypher, B. L., Wingert, C. M., & Job, C. L. V. H. (2005). *Urban roads and the endangered San Joaquin kit fox*. California Department of Transportation.

Bommarco, R., Kleijn, D., & Potts, S. G. (2013). Ecological intensification: Harnessing ecosystem services for food security. *Trends in Ecology & Evolution*, *28*(4), 230–238.

Boryan, C., Yang, Z., Mueller, R., & Craig, M. (2011). Monitoring US agriculture: The US department of agriculture, national agricultural statistics service, cropland data layer program. *Geocarto International*, *26*(5), 341–358.

Bourque, K., Schiller, A., Loyola Angosto, C., McPhail, L., Bagnasco, W., Ayres, A., & Larsen, A. (2019). Balancing agricultural production, groundwater management, and biodiversity goals: A multi-benefit optimization model of agriculture in Kern County, California. *Science of The Total Environment*, *670*, 865–875. https://doi.org/10.1016/j.scitotenv.2019.03.197

Bryant, B. P., Kelsey, T. R., Vogl, A. L., Wolny, S. A., MacEwan, D., Selmants, P. C., Biswas, T., & Butterfield, H. S. (2020). Shaping Land Use Change and Ecosystem Restoration in a Water-Stressed Agricultural Landscape to Achieve Multiple Benefits. *Frontiers in Sustainable Food Systems*, *4*, 138. https://doi.org/10.3389/fsufs.2020.00138

Buto, S. G., & Anderson, R. D. (2020). *NHDPlus High Resolution (NHDPlus HR)—A hydrography framework for the Nation* (Report No. 2020–3033; Fact Sheet, p. 2). USGS Publications Warehouse. https://doi.org/10.3133/fs20203033

California Department of Fish and Wildlife California Interagency Wildlife Task Group. (2016). *Kit Fox Predicted Habitat—CWHR M148 [ds2599].* https://map.dfg.ca.gov/metadata/ds2599.html

California Department of Food and Agriculture. (2019). *California Agricultural Statistics Review 2018-2019.* https://www.cdfa.ca.gov/statistics/PDFs/2018-2019AgReportnass.pdf

California Department of Water Resources. (2017). *2014 California Statewide Agricultural Land Use*. https://gis.water.ca.gov/app/CADWRLandUseViewer/

California Department of Water Resources. (2019). *2016 California Statewide Agricultural Land Use*. https://gis.water.ca.gov/app/CADWRLandUseViewer/

California Department of Water Resources. (2021). *Sustainable Groundwater Management Grant Program*. https://water.ca.gov/Work-With-Us/Grants-And-Loans/Sustainable-Groundwater

Cypher, B. L., Kelly, P. A., Williams, D. F., Clark, H. O., Brown, A. D., & Phillips, S. E. (2005). *Foxes in farmland: Recovery of the endangered San Joaquin kit fox on private lands in California* [FINAL REPORT SUBMITTED TO THE NATIONAL FISH AND WILDLIFE FOUNDATION]. https://esrp.csustan.edu/publications/pdf/nfwf_esrp_kitfox.pdf

Cypher, B. L., Phillips, S. E., & Kelly, P. A. (2007). *Habitat Suitability and Potential Corridors for San Joaquin Kit Fox in the San Luis Unit*. 38.

Cypher, B. L., Phillips, S. E., & Kelly, P. A. (2013). Quantity and distribution of suitable habitat for endangered San Joaquin kit foxes: Conservation implications. *Canid Biology and Conservation*, *16*, 25–31.

Cypher, B. L., & Van Horn Job, C. L. (2012). *Management and conservation of San Joaquin kit foxes in urban environments*. *25*(25).

Cypher, B. L., Warrick, G. D., Otten, M. R., O'Farrell, T. P., Berry, W. H., Harris, C. E., Kato, T. T., McCue, P. M., Scrivner, J. H., & Zoellick, B. W. (2000). Population dynamics of San Joaquin kit foxes at the Naval Petroleum Reserves in California. *Wildlife Monographs*, 1–43.

Cypher, B. L., Westall, T. L., Spencer, K. A., Meade, D. E., Kelly, E. C., Dart, J., & Van Horn Job, C. L. (2019). *Response of San Joaquin kit foxes to Topaz Solar Farms: Implications for conservation of kit foxes. BHE Renewables and Topaz Solar Farms. Final Report.*

D'Aloia, C. C., Naujokaitis-Lewis, I., Blackford, C., Chu, C., Curtis, J. M., Darling, E., Guichard, F., Leroux, S. J., Martensen, A. C., & Rayfield, B. (2019). Coupled networks of permanent protected areas and dynamic conservation areas for biodiversity conservation under climate change. *Frontiers in Ecology and Evolution*, *7*, 27. https://doi.org/10.3389/fevo.2019.00027

Department of Water Resources. (2021, September 5). *Canals and Aqueducts Local*. https://atlas-dwr.opendata.arcgis.com/datasets/b788fb2628844f54b92e46dac5bb7229_

Dickson, B. G., Albano, C. M., McRae, B. H., Anderson, J. J., Theobald, D. M., Zachmann, L. J., Sisk, T. D., & Dombeck, M. P. (2017). Informing Strategic Efforts to Expand and Connect Protected Areas Using a Model of Ecological Flow, with Application to the Western United States. *Conservation Letters*, *10*(5), 564–571. https://doi.org/10.1111/conl.12322

Diniz, M. F., Cushman, S. A., Machado, R. B., & Júnior, P. D. M. (2020). Landscape connectivity modeling from the perspective of animal dispersal. *Landscape Ecology*, *35*(1), 41–58.

Doherty, T. S., & Driscoll, D. A. (2018). Coupling movement and landscape ecology for animal conservation in production landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *285*(1870), 20172272.

Dudley, N., & Alexander, S. (2017). Agriculture and biodiversity: A review. *Biodiversity*, *18*(2–3), 45–49.

Fahrig, L. (2007). Non-optimal animal movement in human-altered landscapes. *Functional Ecology*, *21*(6), 1003–1015.

Feniuk, C., Balmford, A., & Green, R. E. (2019). Land sparing to make space for species dependent on natural habitats and high nature value farmland. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1909), 20191483. https://doi.org/10.1098/rspb.2019.1483

Fischer, J., Abson, D. J., Bergsten, A., Collier, N. F., Dorresteijn, I., Hanspach, J., Hylander, K., Schultner, J., & Senbeta, F. (2017). Reframing the food–biodiversity challenge. *Trends in Ecology & Evolution*, *32*(5), 335–345.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., & Gibbs, H. K. (2005). Global consequences of land use. *Science*, *309*(5734), 570–574. https://doi.org/10.1126/science.1111772

Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., Mueller, N. D., O'Connell, C., Ray, D. K., West, P. C., Balzer, C., Bennett, E. M., Carpenter, S. R., Hill, J., Monfreda, C., Polasky, S., Rockström, J., Sheehan, J., Siebert, S., … Zaks, D. P. M. (2011). Solutions for a cultivated planet. *Nature*, *478*(7369), 337–342. https://doi.org/10.1038/nature10452

Folke, C. (2006). The Economic Perspective: Conservation against Development versus Conservation for Development. *Conservation Biology*, *20*(3), 686–688. https://doi.org/10.1111/j.1523-1739.2006.00446.x

Fraterrigo, J. M., Pearson, S. M., & Turner, M. G. (2009). Joint effects of habitat configuration and temporal stochasticity on population dynamics. *Landscape Ecology*, *24*(7), 863–877.

Frei, B., Queiroz, C., Chaplin-Kramer, B., Andersson, E., Renard, D., Rhemtulla, J. M., & Bennett, E. M. (2020). A brighter future: Complementary goals of diversity and multifunctionality to build resilient agricultural landscapes. *Global Food Security*, *26*, 100407. https://doi.org/10.1016/j.gfs.2020.100407

Gebremichael, M., Krishnamurthy, P. K., Ghebremichael, L. T., & Alam, S. (2021). What Drives Crop Land Use Change during Multi-Year Droughts in California's Central Valley? Prices or Concern for Water? *Remote Sensing*, *13*(4), 650. https://doi.org/10.3390/rs13040650

Gesch, D. B., Evans, G. A., Oimoen, M. J., & Arundel, S. (2018). *The National Elevation Dataset* (pp. 83–110). American Society for Photogrammetry and Remote Sensing; USGS Publications Warehouse. http://pubs.er.usgs.gov/publication/70201572

Golet, G. H., Low, C., Avery, S., Andrews, K., McColl, C. J., Laney, R., & Reynolds, M. D. (2018). Using ricelands to provide temporary shorebird habitat during migration. *Ecological Applications*, *28*(2), 409–426. https://doi.org/10.1002/eap.1658

Griffin, D., & Anchukaitis, K. J. (2014). How unusual is the 2012–2014 California drought? *Geophysical Research Letters*, *41*(24), 9017–9023.

Griffith, G. E., Omernik, J. M., Smith, D. W., Cook, T. D., Tallyn, E., Moseley, K., & Johnson, C. B. (2016). *Ecoregions of California* (Report No. 2016–1021; Open-File Report). USGS Publications Warehouse. https://doi.org/10.3133/ofr20161021

Haight, R. G., Cypher, B., Kelly, P. A., Phillips, S., Ralls, K., & Possingham, H. P. (2004). Optimizing reserve expansion for disjunct populations of San Joaquin kit fox. *Biological Conservation*, *117*(1), 61–72.

Hanak, E., Escriva-Bou, A., Gray, B., Green, S., Harter, T., Jezdimirovic, J., Lund, J., Medellín-Azuara, J., Moyle, P., & Seavy, N. (2019). Water and the future of the San Joaquin Valley. *Public Policy Institute of California: San Francisco, CA, USA*.

Hannah, L., Midgley, G., Andelman, S., Araújo, M., Hughes, G., Martinez-Meyer, E., Pearson, R., & Williams, P. (2007). Protected area needs in a changing climate. *Frontiers in Ecology and the Environment*, *5*(3), 131–138. https://doi.org/10.1890/1540-9295(2007)5[131:PANIAC]2.0.CO;2

Harrison, S. (2013). *Plant and Animal Endemism in California*. University of California Press. https://doi.org/10.1525/9780520954731

Jin, S., Homer, C., Yang, L., Danielson, P., Dewitz, J., Li, C., Zhu, Z., Xian, G., & Howard, D. (2019). Overall methodology design for the United States national land cover database 2016 products. *Remote Sensing*, *11*(24), 2971.

Kattwinkel, M., Biedermann, R., & Kleyer, M. (2011). Temporary conservation for urban biodiversity. *Biological Conservation*, *144*(9), 2335–2343. https://doi.org/10.1016/j.biocon.2011.06.012

Keeley, A. T., Beier, P., & Gagnon, J. W. (2016). Estimating landscape resistance from habitat suitability: Effects of data source and nonlinearities. *Landscape Ecology*, *31*(9), 2151–2162. https://doi.org/10.1007/s10980-016-0387-5

Keeley, A. T., Beier, P., Keeley, B. W., & Fagan, M. E. (2017). Habitat suitability is a poor proxy for landscape connectivity during dispersal and mating movements. *Landscape and Urban Planning*, *161*, 90–102. https://doi.org/10.1016/j.landurbplan.2017.01.007

Kelsey, R., Hart, A., Butterfield, H. S., & Vink, D. (2018). Groundwater sustainability in the San Joaquin Valley: Multiple benefits if agricultural lands are retired and restored strategically. *California Agriculture*, *72*(3), 151–154.

Koopman, M. E., Cypher, B. L., & Scrivner, J. H. (2000). Dispersal Patterns of San Joaquin Kit Foxes (Vulpes Macrotis Mutica). *Journal of Mammalogy*, *81*(1), 213–222. https://doi.org/10.1644/1545-1542(2000)081<0213:DPOSJK>2.0.CO;2

Kopittke, P. M., Menzies, N. W., Wang, P., McKenna, B. A., & Lombi, E. (2019). Soil and the intensification of agriculture for global food security. *Environment International*, *132*, 105078. https://doi.org/10.1016/j.envint.2019.105078

Kremen, C., & Miles, A. (2012). Ecosystem services in biologically diversified versus conventional farming systems: Benefits, externalities, and trade-offs. *Ecology and Society*, *17*(4).

Kuussaari, M., Hyvönen, T., & Härmä, O. (2011). Pollinator insects benefit from rotational fallows. *Agriculture, Ecosystems & Environment*, *143*(1), 28–36. https://doi.org/10.1016/j.agee.2011.03.006

Larrosa, C., Carrasco, L. R., & Milner-Gulland, E. (2016). Unintended feedbacks: Challenges and opportunities for improving conservation effectiveness. *Conservation Letters*, *9*(5), 316–326. https://doi.org/10.1111/conl.12240

Larsen, A. E., Farrant, D. N., & MacDonald, A. J. (2020). Spatiotemporal overlap of pesticide use and species richness hotspots in California. *Agriculture, Ecosystems & Environment*, *289*, 106741. https://doi.org/10.1016/j.agee.2019.106741

Larsen, A. E., & McComb, S. (2021). Land cover and climate changes drive regionally heterogeneous increases in US insecticide use. *Landscape Ecology*, *36*(1), 159–177. https://doi.org/10.1007/s10980-020-01130-5

Larsen, A. E., Meng, K., & Kendall, B. E. (2019). Causal analysis in control–impact ecological studies with observational data. *Methods in Ecology and Evolution*, *10*(7), 924–934. https://doi.org/10.1111/2041-210X.13190

Lawler, J., Ruesch, A. S., Olden, J., & McRae, B. (2013). Projected climate-driven faunal movement routes. *Ecology Letters*, *16*(8), 1014–1022.

Lortie, C. J., Filazzola, A., Kelsey, R., Hart, A. K., & Butterfield, H. S. (2018). Better late than never: A synthesis of strategic land retirement and restoration in California. *Ecosphere*, *9*(8), e02367. https://doi.org/10.1002/ecs2.2367

Maxwell, S. L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A. S. L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B. B. N., Wenger, A., Jonas, H. D., Venter, O., & Watson, J. E. M. (2020). Area-based conservation in the twenty-first century. *Nature*, *586*(7828), 217–227. https://doi.org/10.1038/s41586-020-2773-z

McRae, B. H. (2013). *Circuitscape ArcGIS toolbox*. https://circuitscape.org/downloads/

McRae, B. H., Dickson, B. G., Keitt, T. H., & Shah, V. B. (2008). Using circuit theory to model connectivity in ecology, evolution, and conservation. *Ecology*, *89*(10), 2712–2724.

McRae, B. H., Hall, S. A., Beier, P., & Theobald, D. M. (2012). Where to Restore Ecological Connectivity? Detecting Barriers and Quantifying Restoration Benefits. *PLoS ONE*, *7*(12), e52604. https://doi.org/10.1371/journal.pone.0052604

McRae, B. H., & Kavanagh, D. M. (2011). Linkage mapper connectivity analysis software. *The Nature Conservancy, Seattle WA*.

McRae, B. H., & Kavanagh, D. M. (2017). *User Guide: Linkage Pathways Tool of the Linkage Mapper Toolbox. Version 2.0*.

McRae, B. H., & Shah, V. B. (2009). Circuitscape user's guide. *The University of California, Santa Barbara*.

McRae, B. H., Shah, V., & Edelman, A. (2016). *Circuitscape: Modeling landscape connectivity to promote conservation and human health*. https://doi.org/10.13140/RG.2.1.4265.1126

Medellín-Azuara, J., MacEwan, D., Howitt, R. E., Koruakos, G., Dogrul, E. C., Brush, C. F., Kadir, T. N., Harter, T., Melton, F., & Lund, J. R. (2015). Hydro-economic analysis of groundwater pumping for irrigated agriculture in California's Central Valley, USA. *Hydrogeology Journal*, *23*(6), 1205–1216.

Medellín-Azuara, J., MacEwan, D., Howitt, R. E., Sumner, D. A., Lund, J. R., Scheer, J., Gailey, R., Hart, Q., Alexander, N. D., & Arnold, B. (2016). Economic analysis of the 2016 California drought on agriculture. *Center for Watershed Sciences. Davis, CA: UC Davis*.

Melton, F. (2020). *Personal Correspondence* [Personal communication].

Melton, F., Rosevelt, C., Guzman, A., Johnson, L., Zaragoza, I., Verdin, J., Thenkabail, P., Wallace, C., Mueller, R., & Willis, P. (2015). Fallowed area mapping for drought impact reporting: 2015 assessment of conditions in the California Central Valley. *NASA Ames Research Center: Mountain View, CA, USA*. https://nex.nasa.gov/nex/projects/1372/

Mockshell, J., & Kamanda, J. (2018). Beyond the agroecological and sustainable agricultural intensification debate: Is blended sustainability the way forward? *International Journal of Agricultural Sustainability*, *16*(2), 127–149. https://doi.org/10.1080/14735903.2018.1448047

Moilanen, A., Laitila, J., Vaahtoranta, T., Dicks, L. V., & Sutherland, W. J. (2014). Structured analysis of conservation strategies applied to temporary conservation. *Biological Conservation*, *170*, 188–197. https://doi.org/10.1016/j.biocon.2014.01.001

Moose, P. B. (2021). *San Joaquin kit fox male*. Public Domain Images Website. http://www.public-domain-image.com/full-image/fauna-animals-public-domain-images-pictures/foxes-and-wolves-public-domain-images-pictures/san-joaquin-kit-fox-male.jpg.html

Nogeire-McRae, T., Lawler, J. J., Schumaker, N. H., Cypher, B. L., & Phillips, S. E. (2019). Land use change and rodenticide exposure trump climate change as the biggest stressors to San Joaquin kit fox. *PLOS ONE*, *14*(6), e0214297. https://doi.org/10.1371/journal.pone.0214297

Norris, K. (2008). Agriculture and biodiversity conservation: Opportunity knocks. *Conservation Letters*, *1*(1), 2–11.

Office of Governor Gavin Newsom. (2020). *Governor Newsom Launches Innovative Strategies to Use California Land to Fight Climate Change, Conserve Biodiversity and Boost Climate Resilience*.

Oliver, Y. M., Robertson, M. J., & Weeks, C. (2010). A new look at an old practice: Benefits from soil water accumulation in long fallows under Mediterranean conditions. *Agricultural Water Management*, *98*(2), 291–300.

Phalan, B., Onial, M., Balmford, A., & Green, R. E. (2011). Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. *Science*, *333*(6047), 1289–1291. https://doi.org/10.1126/science.1208742

Queiroz, C., Beilin, R., Folke, C., & Lindborg, R. (2014). Farmland abandonment: Threat or opportunity for biodiversity conservation? A global review. *Frontiers in Ecology and the Environment*, *12*(5), 288–296.

R Core Team. (2019). *R: A language and environment for statistical computing. R Foundation for Statistical Computing.* https://www.R-project.org/.

Raymond, C. M., Frantzeskaki, N., Kabisch, N., Berry, P., Breil, M., Nita, M. R., Geneletti, D., & Calfapietra, C. (2017). A framework for assessing and implementing the co-benefits of nature-based solutions in urban areas. *Environmental Science & Policy*, *77*, 15–24. https://doi.org/10.1016/j.envsci.2017.07.008

Reynolds, M. D., Sullivan, B. L., Hallstein, E., Matsumoto, S., Kelling, S., Merrifield, M., Fink, D., Johnston, A., Hochachka, W. M., & Bruns, N. E. (2017). Dynamic conservation for migratory species. *Science Advances*, *3*(8), e1700707.

Ribaudo, M., Greene, C., Hansen, L., & Hellerstein, D. (2010). Ecosystem services from agriculture: Steps for expanding markets. *Ecological Economics*, *69*(11), 2085–2092.

Roberts, M., Milman, A., & Blomquist, W. (2021). The Sustainable Groundwater Management Act (SGMA): California's Prescription for Common Challenges of Groundwater Governance. In J. Baird & R. Plummer (Eds.), *Water Resilience: Management and Governance in Times of Change* (pp. 41–63). Springer International Publishing. https://doi.org/10.1007/978-3-030-48110-0_3

Rolf, W., Pauleit, S., & Wiggering, H. (2019). A stakeholder approach, door opener for farmland and multifunctionality in urban green infrastructure. *Urban Forestry & Urban Greening*, *40*, 73–83. https://doi.org/10.1016/j.ufug.2018.07.012

Sanz-Pérez, A., Giralt, D., Robleño, I., Bota, G., Milleret, C., Mañosa, S., & Sardà-Palomera, F. (2019). Fallow management increases habitat suitability for endangered steppe bird species through changes in vegetation structure. *Journal of Applied Ecology*, *56*(9), 2166–2175.

Saura, S., Bodin, Ö., & Fortin, M. (2014). EDITOR'S CHOICE: Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks. *Journal of Applied Ecology*, *51*(1), 171–182.

Shackelford, G. E., Steward, P. R., German, R. N., Sait, S. M., & Benton, T. G. (2015). Conservation planning in agricultural landscapes: Hotspots of conflict between agriculture and nature. *Diversity and Distributions*, *21*(3), 357–367.

California water code [CWC]. Division 6, part 2.74. Sustainable Groundwater Management., (2014).

Stewart, J. A. E., Butterfield, H. S., Richmond, J. Q., Germano, D. J., Westphal, M. F., Tennant, E. N., & Sinervo, B. (2019). Habitat restoration opportunities, climatic niche contraction, and conservation biogeography in California's San Joaquin Desert. *PLOS ONE*, *14*(1), e0210766. https://doi.org/10.1371/journal.pone.0210766

Tarjuelo, R., Margalida, A., & Mougeot, F. (2020). Changing the fallow paradigm: A win–win strategy for the post-2020 Common Agricultural Policy to halt farmland bird declines. *Journal of Applied Ecology*, *57*(3), 642–649.

Tilman, D., Balzer, C., Hill, J., & Befort, B. L. (2011). Global food demand and the sustainable intensification of agriculture. *Proceedings of the National Academy of Sciences*, *108*(50), 20260. https://doi.org/10.1073/pnas.1116437108

Toivonen, M., Herzon, I., & Helenius, J. (2013). Environmental fallows as a new policy tool to safeguard farmland biodiversity in Finland. *Biological Conservation*, *159*, 355–366.

Trainor, A. M., Walters, J. R., Morris, W. F., Sexton, J., & Moody, A. (2013). Empirical estimation of dispersal resistance surfaces: A case study with red-cockaded woodpeckers. *Landscape Ecology*, *28*(4), 755–767.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters*, *8*(8), 857–874.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., … Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*(6374), 466–469. https://doi.org/10.1126/science.aam9712

United States Geological Survey (USGS). (2018). *National Elevation Dataset*. The National Map. https://viewer.nationalmap.gov/advanced-viewer/

United States Geological Survey (USGS). (2020). *National Hydrography Dataset: NHDPlus High Resolution (NHDPlus HR)*. https://www.usgs.gov/core-science-systems/ngp/national-hydrography/access-national-hydrography-products

U.S. Census Bureau. (2019). *TIGER/Line Shapefiles (machinereadable data files): California, Primary and Secondary Roads*.

U.S. Fish and Wildlife. (2020). *Species Status Assessment Report for the San Joaquin kit fox (Vulpes macrotis mutica)*. https://ecos.fws.gov/ServCat/DownloadFile/185116

U.S. Fish and Wildlife Service. (1998). *Recovery plan for upland species of the San Joaquin Valley, California*. U.S. Fish and Wildlife Service. https://esrp.csustan.edu/publications/recoveryplan.php

Venter, O., Magrach, A., Outram, N., Klein, C. J., Possingham, H. P., Di Marco, M., & Watson, J. E. M. (2018). Bias in protected-area location and its effects on long-term aspirations of biodiversity conventions: Protected Areas Missing Biodiversity. *Conservation Biology*, *32*(1), 127–134. https://doi.org/10.1111/cobi.12970

Villard, M., & Metzger, J. P. (2014). Beyond the fragmentation debate: A conceptual model to predict when habitat configuration really matters. *Journal of Applied Ecology*, *51*(2), 309–318.

Ward, M., Saura, S., Williams, B., Ramírez-Delgado, J. P., Arafeh-Dalmau, N., Allan, J. R., Venter, O., Dubois, G., & Watson, J. E. M. (2020). Just ten percent of the global terrestrial protected area network is structurally connected via intact land. *Nature Communications*, *11*(1), 4563. https://doi.org/10.1038/s41467-020-18457-x

Warrick, G. D., Clark, H. O., Kelly, P. A., Williams, D. F., & Cypher, B. L. (2007). Use of Agricultural Lands by San Joaquin Kit Foxes. *Western North American Naturalist*, *67*(2), 270–277. JSTOR.

Warrick, G. D., & Cypher, B. L. (1998). Factors Affecting the Spatial Distribution of San Joaquin Kit Foxes. *The Journal of Wildlife Management*, *62*(2), 707. https://doi.org/10.2307/3802347

White, P. J., & Garrott, R. A. (1999). Population dynamics of kit foxes. *Canadian Journal of Zoology*, *77*(3), 486–493. https://doi.org/10.1139/z99-007

White, P. J., & Ralls, K. (1993). Reproduction and spacing patterns of kit foxes relative to changing prey availability. *The Journal of Wildlife Management*, 861–867.

White, P. J., Ralls, K., & Vanderbilt-White, C. A. (1995). Overlap in habitat and food use between coyotes and San Joaquin kit foxes. *Southwestern Naturalist*, *40*, 342–349.

Wooldridge, J. M. (2010). *Econometric analysis of cross section and panel data* (2nd ed). MIT Press.

Zeller, K. A., Jennings, M. K., Vickers, T. W., Ernest, H. B., Cushman, S. A., & Boyce, W. M. (2018). Are all data types and connectivity models created equal? Validating common connectivity approaches with dispersal data. *Diversity and Distributions*, *24*(7), 868–879. https://doi.org/10.1111/ddi.12742

Zeller, K. A., Lewsion, R., Fletcher, R. J., Tulbure, M. G., & Jennings, M. K. (2020). Understanding the Importance of Dynamic Landscape Connectivity. *Land*, *9*(9), 303.

Figure 1

Click here to access/download;Figure;Figure1.png

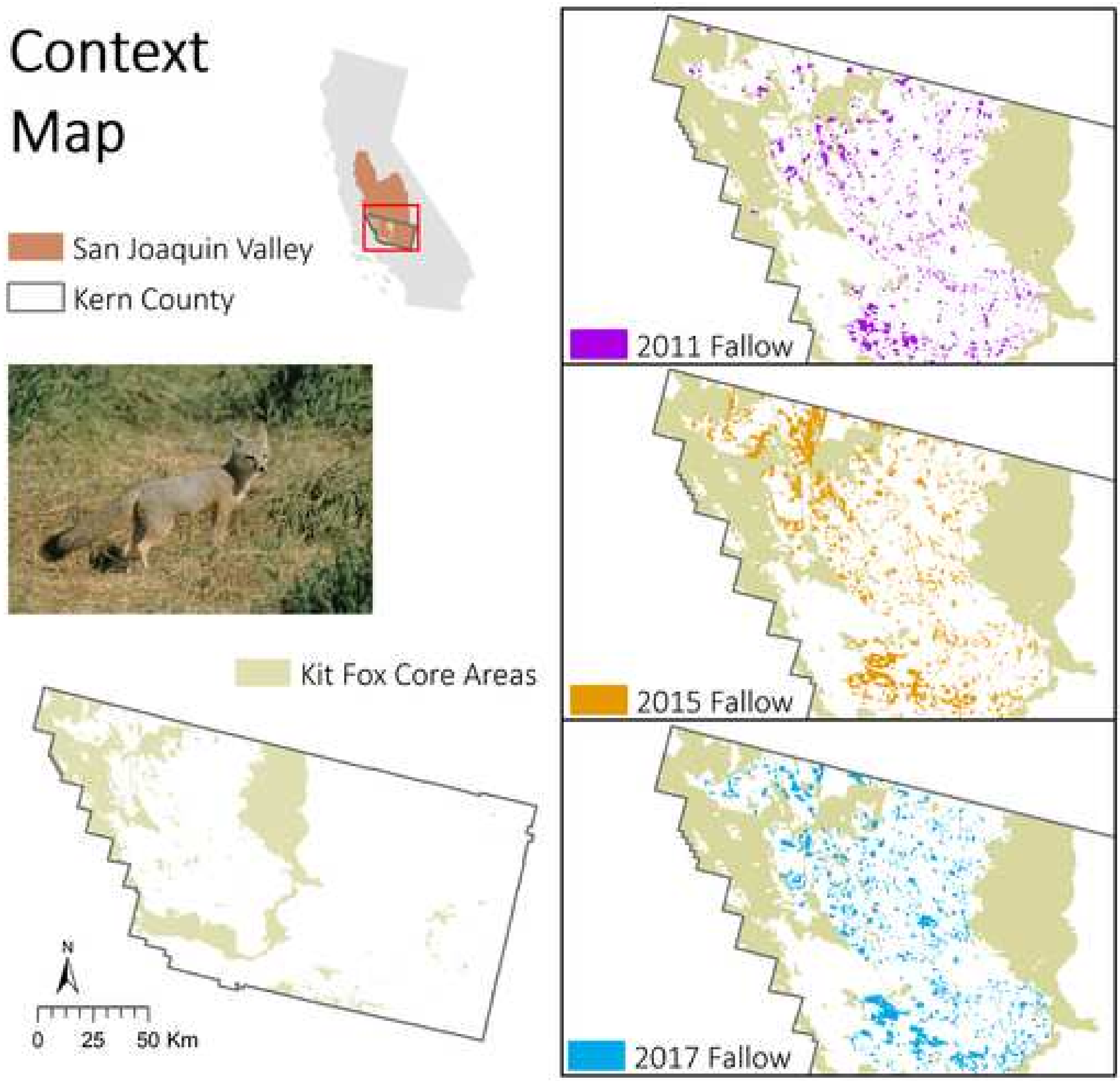

Figure 2

Click here to access/download;Figure;Figure2.png

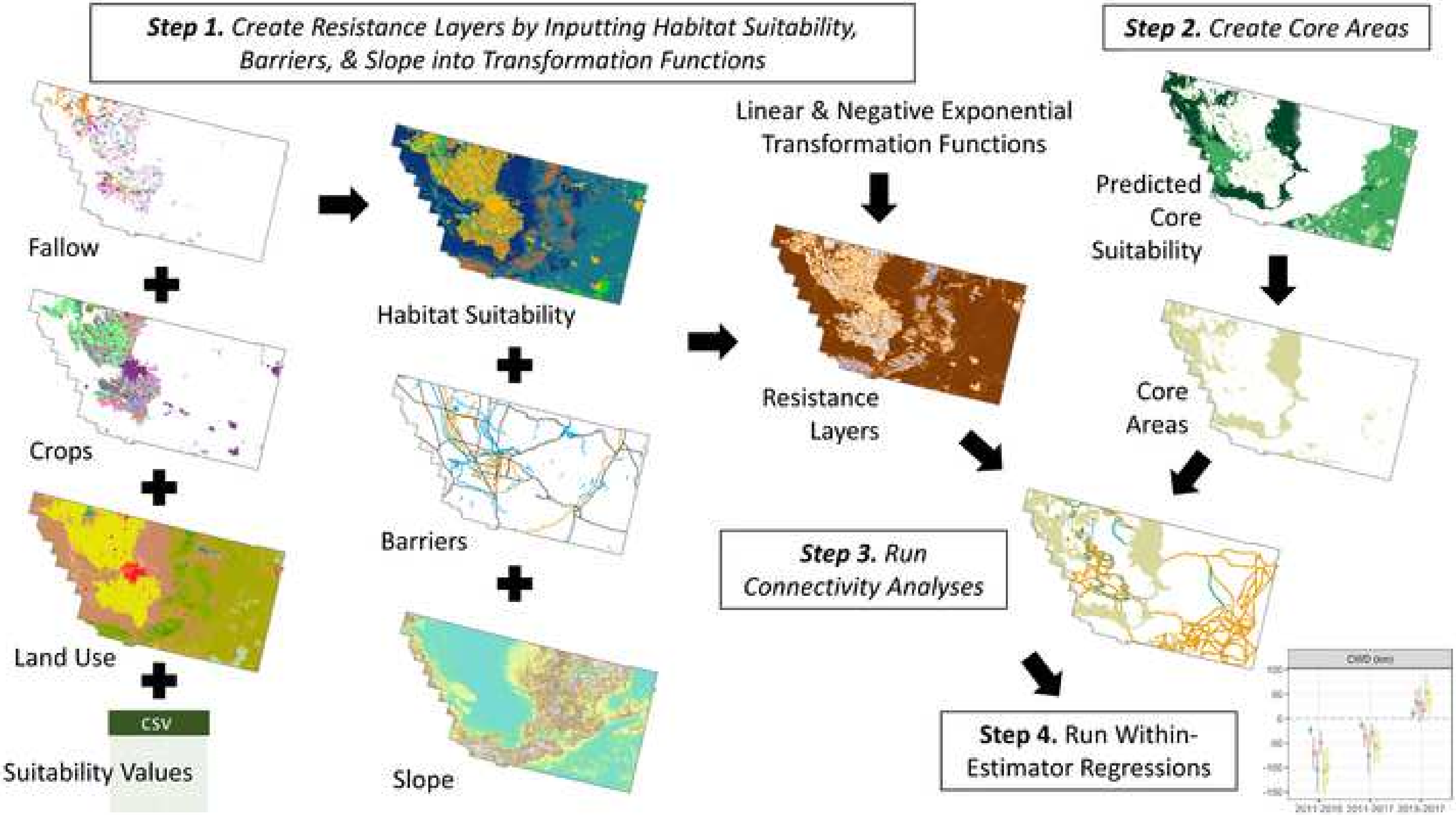

Figure 3

Click here to access/download;Figure;Figure3.png

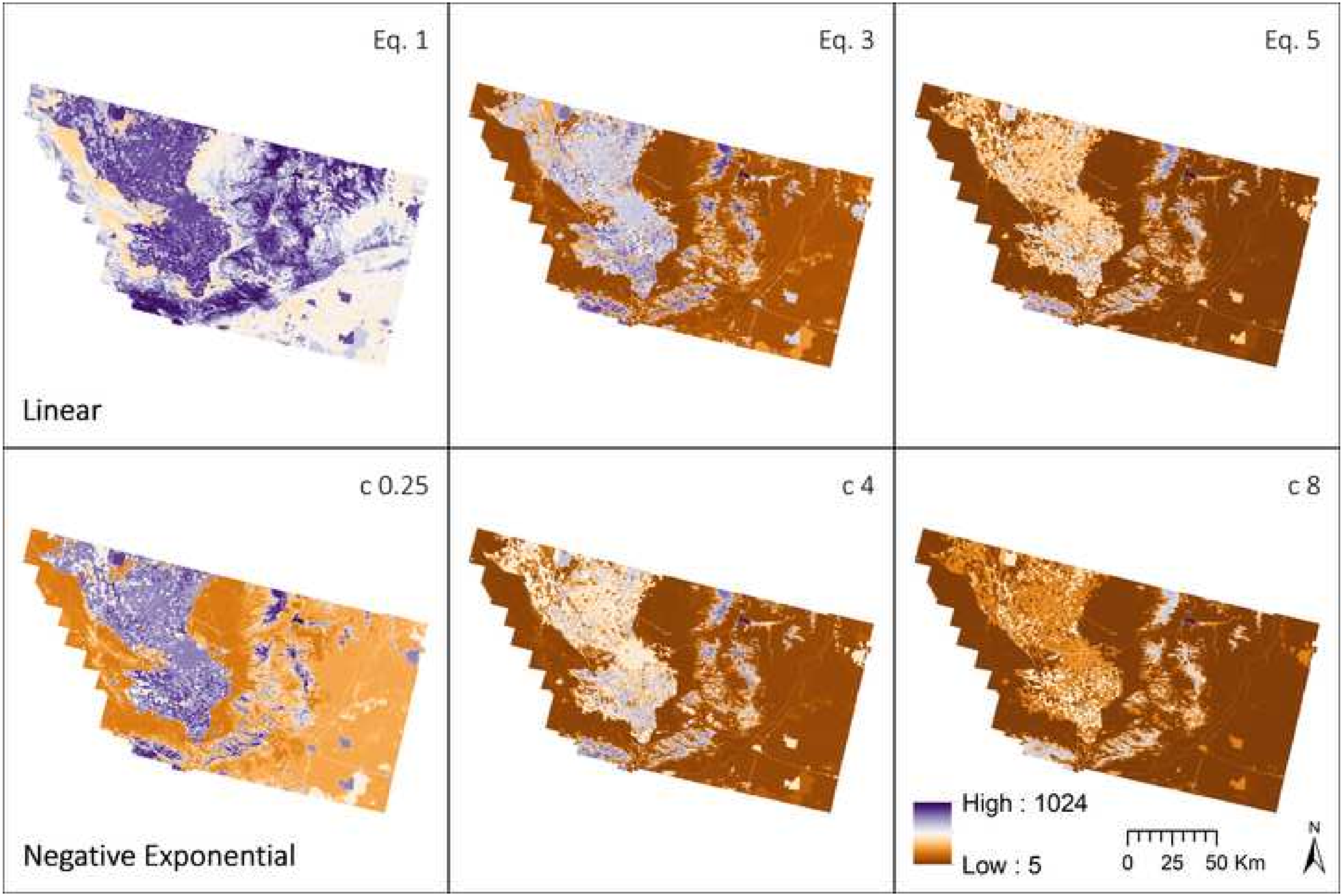

Figure 4

Click here to access/download;Figure;Figure4.jpg

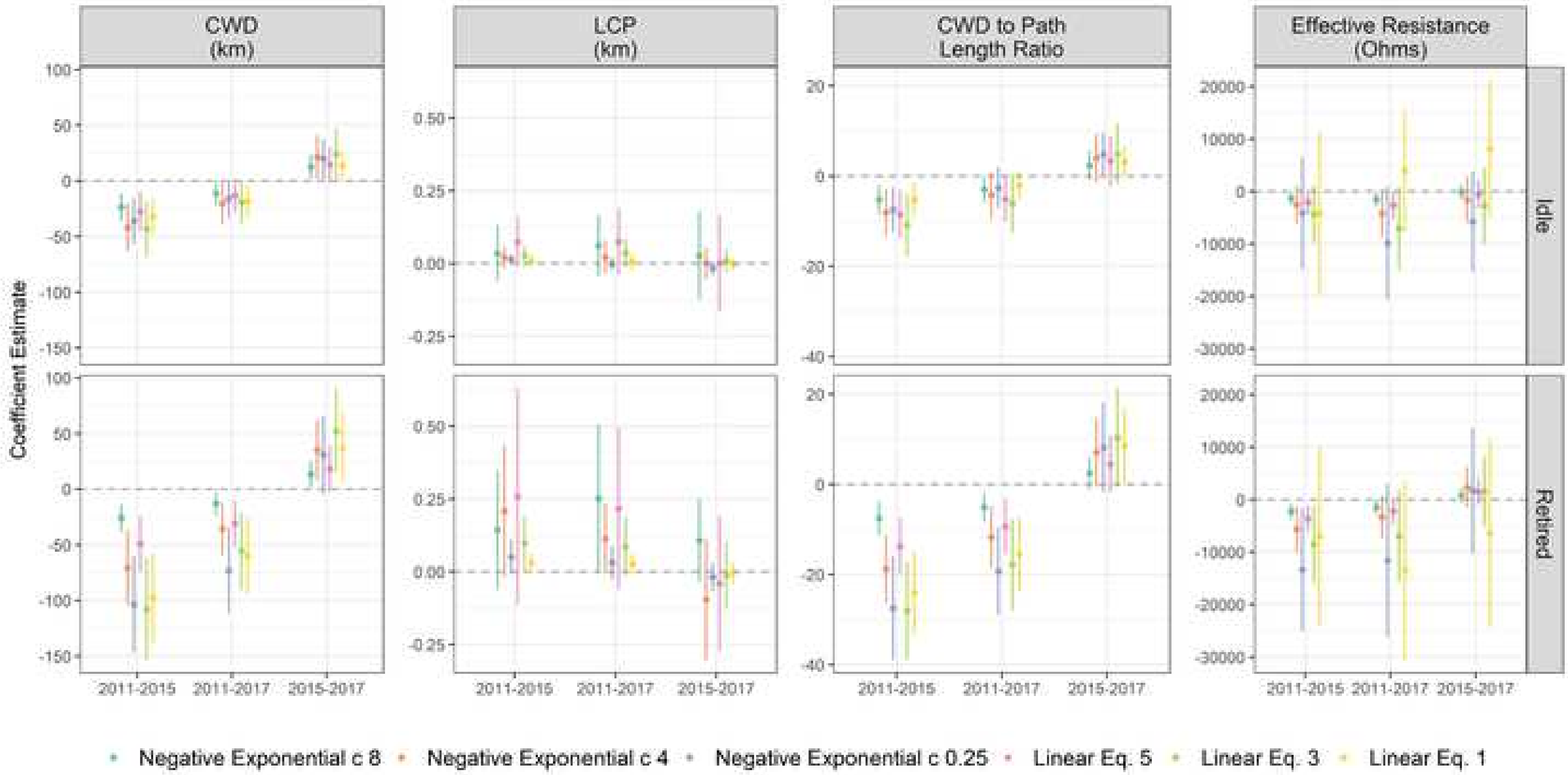

Table 1. Pearson correlation values between all 6 resistance models for 2011 for fallow defined as idle farmland.

	Eq. 1	**Eq. 3**	**Eq. 5**	**c 0.25**	**c 4**	**c 8**
Linear Eq. 1	1					
Linear Eq. 3	0.74	1				
Linear Eq. 5	0.73	0.97	1			
Negative Exponential c 0.25	0.73	0.99	0.94	1		
Negative Exponential c 4	0.74	0.99	1.00	0.97	1	
Negative Exponential c 8	0.70	0.92	0.98	0.88	0.97	1

Response to Editor

COMMENTS FOR THE AUTHOR:

Dear Dr. McComb,

Thank you for your submission "Evaluating Climate-Driven Fallowing for Ecological Connectivity of Species at Risk." This article is looking very good. Thanks for all the work that you have done in this interesting and well-written research. I have two small last suggestions and then I believe it is ready for publication.

Thank you so much for all your help and support throughout this process.

The main takeaway seems to me to be that drought and policy-driven fallowing results in increased fallowing. The dynamic nature of the fallowing seems less clear in the study. I believe the manuscript has moved to clarify these conclusions. Thank you. Modeling habitat with two separate (idle vs retired) fallow scores is a good response to reviewer's apt concern that it is self-fulfilling that, by definition, setting a higher suitability score for fallowed lands, will automatically result in outputs that have increased connectivity. Please make sure this comparison and results are prominently presented. Consider including in the abstract (these results are not mentioned now) a statement like "the benefits were on average more than 2.5 times greater with longer-term fallowing." Could you also please take a last look at the use of temporary in the article and confirm that it is consistent with your final revised message?

Thank you so much. We have ensured that all results are now presented clearly and consistently throughout the paper, particularly between the two fallowing scenarios. We have further highlighted the comparison between shorter-term, transitory idle fallow lands and longer-term, semi-permanent retired fallow lands throughout the paper. We have added a few lines throughout the results section highlighting the differences in shorter versus longer term fallowing results for each metric and across metrics (Lines 482-485, 494-496, 509-515), and then included a line in the abstract (Lines 56-59) and updated the relevant lines in the discussion (Lines 560-561, 639-644) to further support that comparison. We have updated or removed the use of the word temporary throughout—often with the use of the words temporarily or transitory—to hopefully better reflect the final message and the difference between the two fallow scenarios, both of which can be dynamic and temporary in a sense, but one of which is of a longer and more semi-permanent duration (retired) than the other (idle).

Secondly, while I greatly appreciate your response to reviewers' requests for additional background review, the reference list has become a bit bloated. And there still is a relatively high proportion of articles that are ~20 years old. Can you take one last look through and update/assess essentialness of references especially where have long daisy-chain lists of references at the end of some of your points.

We agree, and have done our best to go through each of the references, and parse down the citations where possible throughout. We have had to leave some of the relevant kit fox articles from the 90's as they were pivotal kit fox tracking or land-use studies, but otherwise we have tried to ensure studies cited are as recent and relevant as possible.

I have added a few small points below. I look forward to receiving your final draft. Thank you again for your work on preparing this paper.

Thank you again for your suggestions, and we have addressed the rest of the specific revisions below.

Best,
Todd Lookingbill
Coordinating Editor

Line 48: Should temporary be used here, as the results are for temporary idle or permanently retired lands?

We have removed the use of the word temporary here (Line 53), as you are correct the results presented are for both, and the word may increase confusion. We have also removed the use of the word throughout the paper in areas where it may cause confusion.

Line 50: "(~0.8–18% and 0.3–12.2% in 2015/2017 respective to 2011" Please provide a brief explanation for the range of values presented, even if simply "for different model scenarios."
We have added "across different model scenarios" to clarify results presented (Line 56).

Line 58: Awkward sentence: "Fallowing-based, agri-environmental programs could help support landowners manage reduced groundwater availability"

We agree and have changed the sentence to read (Lines 65-67): "Agri-environmental programs incentivizing the creation of dynamic, fallowing-based reserves could help landowners manage reduced groundwater availability while improving species' mobility in the face of climate change."

Lines 71 and 111: change "high value" to "high-value"

Changed to "high-value" (Lines 76 & 113).

Line 86: add comma after "Interestingly"

Added comma after “Increasingly” in this line (now Line 91).

Line 149: delete “also” as it is used in the sentence above

Deleted “also” (Line 151).

Figure 1 caption: add “and” before “2017”.

Added “and” (Line 230).

Line 333 and 334: insert space between “Eq.” and “5”.

Inserted the space (Line 338).

Results: There is an occasional shift from past to present tense - e.g., lines 421-425, 465

We read through the results section and ensured all appropriate verbs were in past tense (Lines 419-521). The only lines left in present tense were Lines 465-467—”Thus, while these summaries illustrate overall trends in mobility across the landscape, they do not account for the paired nature of pathways between any given core areas.”—as we believe they were more appropriately phrased this way, but we can change to past tense if needed.

Figure 4 is slightly more difficult to interpret now that it is a two-panel figure. Consider making the top row “retired” and the bottom row “idle,” that would make it easier to compare the same metrics across scenarios. Also consider keeping the y-axes consistent between the retired and idle scenarios to allow for easier comparison.

Thank you for the suggestion, and we have altered the figure to have the idle results on the top row, and the matching retired results on the bottom row, with consistent y-axes, for ease of direct comparison.

Discussion - it strikes me that the reduction in amount of fallowed land from 2015 to 2017 is one of the main pieces of evidence about the “dynamic” nature of the fallowing. Is “retired” land still dynamic. Please review your use of dynamic throughout.

We agree and have ensured the use of “dynamic” is consistent throughout and that it corresponds with the definition we included in the introduction (Lines 115-116, “adaptively managed protected areas with spatial distributions that change through time based on environmental impacts to biodiversity and agricultural production”). We have made sure to clarify in the methods section that retired fallow lands represents longer duration of fallowing than idle, but that both can be used dynamically as the retired fallowing scenario is just longer-term and more semi-permanent than the idle fallowing scenario, resulting in increased recovery and overall suitability from the extended length of fallowing. For instance, a parcel of farmland could be retired for a few years to support connectivity and other ecological benefits, but could later be exchanged with another parcel if that were to improve the spatial arrangement of connectivity corridors due to an alteration in climate, land use, or species condition. We have changed the paragraph describing retired versus idle scenarios to reflect this (Lines 299-310):

“Since the difficulty of traversing fallowed land may differ based on the duration of fallowing (Cypher et al., 2007), we evaluate two different suitability scenarios. First, we consider the suitability of all fallowed lands as "retired", or fallowed for more than one year, to mimic what we might expect in a drought or under SGMA, in which fallow lands are assumed to more closely resemble grassland or shrubland due to a longer duration of fallowing and therefore increased vegetative recovery and habitat suitability in these semi-permanent areas (Cypher et al., 2007, 2013). Second, we evaluated fallowed lands as "idle", or fallowed for one year, in which they are assumed to more closely resemble barren land due to the shorter-term and more transitory nature of fallowing (Cypher et al., 2013). As the distribution of fallowed lands from 2011 to 2017 was likely a combination of these land types, we chose to evaluate these two suitability scenarios to bound our results. Results associated with these two types of fallow land are hereafter referred to as ‘retired’ and ‘idle’ results, respectively.”

We consider both longer-term, semi-permanent fallowed lands and shorter-term, transitory fallowed lands as potential areas for dynamic connectivity reserves, and Lines 646-649 in the discussion try to highlight this point: “Though the opportunity costs of fallowing to farmers under SGMA will likely be high, those costs have the potential to be partially offset by tapping into the conservation potential of dynamic reserves and conservation corridors comprised of either temporarily and/or semi-permanent fallowed lands.”

Line 613: should “layer” be “layers”?

Changed to “layers” (Line 630).

6201 Cecil Green Drive #321
Vancouver, BC Canada V6T 1Z1
Email: smccomb@mail.ubc.ca, shemccomb@gmail.com
Phone: +1 281-435-4865

THE UNIVERSITY OF BRITISH COLUMBIA
Faculty of Forestry

Springer Journals Editorial Office
Landscape Ecology

August 23, 2022

Dear Dr. Todd Lookingbill,

Thank you for the opportunity to revise our manuscript, "Evaluating Climate-Driven Fallowing for Ecological Connectivity of Species At Risk", for consideration in Landscape Ecology. We have undertaken the requested minor revisions of the manuscript.

Our paper evaluates how drought-induced fallowing in Kern County, CA, USA may have influenced connectivity for an endangered species at risk, the San Joaquin kit fox (*Vulpes macrotis mutica*), and highlights the potential for opportunistic and dynamic reserves to improve connectivity via transitory or semi-permanent fallowing. Minor revisions requested included: 1) highlight idle versus retired comparison and results, 2) review use of the words temporary and dynamic throughout, 3) update idle versus retired figure for ease of comparison, 4) condense references, and 5) make necessary grammatical edits. We have made the following changes in response:

- *Idle vs Retired*: We have further highlighted the comparison between shorter-term, transitory idle fallow lands and longer-term, semi-permanent retired fallow lands, adding a few sentences in the results highlighting the differences for each metric and across metrics, updating the relevant lines in the discussion, and adding a statement on the important comparison in the abstract. We have double checked that all results and discussion of results are now presented clearly and consistently throughout the paper.
- *Temporary/Dynamic*: We have checked that the use of the words temporary and dynamic are used consistently and correctly throughout the paper, and have either left as is where appropriate, changed to another word to reduce confusion if deemed necessary, or removed use of the words entirely if not needed.
- *Figure 4*: We have altered Figure 4 so that idle results for each metric are stacked directly above the matching retired results for ease of comparison, and have ensured the y-axes are consistent between the two.
- *References*: We have gone through each of the references, and done our best to parse down the literature cited to the most recent and relevant citations. We made exceptions for a few kit fox articles from the 90's that we deemed essential articles on kit fox, particularly the tracking of kit fox across different land uses.
- *Grammar Edits*: We have made all requested in-line revisions around grammar, punctuation, or phrasing.

We believe our manuscript to be substantially strengthened as a result of the review process and of great interest to your readers. Thank you for your consideration, and for all your help and support throughout this process.

Sincerely,

Sofie McComb & Co-Authors