CONSERVATION PRACTICE AND POLICY

Conservation Biology

A landscape-scale framework to identify refugia from multiple stressors

Isabel M. Rojas[1] │ Megan K. Jennings[1,2] │ Erin Conlisk[1,3] │
Alexandra D. Syphard[4,5,6] │ Jack Mikesell[7] │ Alicia M. Kinoshita[7] │ Krista West[4] │
Doug Stow[4] │ Emanuel Storey[4] │ Mark E. De Guzman[1,8] │ Diane Foote[1,9] │
Alexandria Warneke[10] │ Amber Pairis[10] │ Sherry Ryan[9] │ Lorraine E. Flint[11] │
Alan L. Flint[11] │ Rebecca L. Lewison[1,2]

[1] Department of Biology, San Diego State University, San Diego, California, USA

[2] Institute for Ecological Monitoring and Management, San Diego State University, San Diego, California, USA

[3] Point Blue Conservation Science, Petaluma, California, USA

[4] Department of Geography, San Diego State University, San Diego, California, USA

[5] Vertus Wildfire, San Diego, California, USA

[6] Conservation Biology Institute, La Mesa, California, USA

[7] Department of Civil, Construction, & Environmental Engineering, San Diego State University, San Diego, California, USA

[8] Department of Environmental Science and Policy, University of California, Davis, Davis, California, USA

[9] School of Public Affairs, San Diego State University, San Diego, California, USA

[10] Climate Science Alliance, San Diego, California, USA

[11] Water Resources Discipline, U.S. Geological Survey, Sacramento, California, USA (Email: leflint@sbcglobal.net; alflint@sbcglobal.net)

Current Correspondence
Isabel M. Rojas, Centro de Desarrollo Local, Pontificia Universidad Católica de Chile - Campus Villarrica, Bernardo O'Higgins 501, Villarrica, Chile.
Email: imrojas@uc.cl

Article impact statement: Identifying refugia from multiple stressors can inform conservation plans that aim to protect biodiversity in a changing world.

Abstract

From a conservation perspective, quantifying potential refugial capacity has been predominantly focused on climate refugia, which is critical for maintaining the persistence of species and ecosystems. However, protection from other stressors, such as human-induced changes in fire and hydrology, that cause habitat loss, degradation, and fragmentation is also necessary to ensure that conservation efforts focused on climate are not undermined by other threats. Thus, conceptual and methodological advances for quantifying potential refugia from multiple anthropogenic stressors are important to support conservation efforts. We devised a new conceptual approach, the domains of refugia, for assessing refugial capacity that identifies areas where exposure to multiple stressors is low. In our framework, patterns of environmental variability (e.g., increased frequency of warm summers), thresholds of resilience, and extent and intensity of stressors are used to identify areas of potential refugia from a suite of ongoing anthropogenic stressors (e.g., changes in fire regime). To demonstrate its utility, we applied the framework to a Southern California landscape. Sites with high refugial capacity (super-refugia sites) had on average 30% fewer extremely warm summers, 20% fewer fire events, 10% less exposure to altered river channels and riparian areas, and 50% fewer recreational trails than the surrounding landscape. Our results suggest that super-refugia sites (∼8200 km²) for some natural communities are

underrepresented in the existing protected area network, a finding that can inform efforts to expand protected areas. Our case study highlights how considering exposure to multiple stressors can inform planning and practice to conserve biodiversity in a changing world.

KEYWORDS

amenazas, biodiversidad, cambio climático, cambio global, gestión y planificación estratégica, paisajes, sur de California

Marco Conceptual a para Identificar Refugios de Múltiples Amenazas a Escala de Paisaje

Resumen: Desde la perspectiva de la conservación, la cuantificación de la capacidad potencial de refugio se ha enfocado principalmente en los refugios climáticos, los cuales son críticos para mantener la persistencia de las especies y los ecosistemas. Sin embargo, la protección ante otros factores estresantes, como los cambios inducidos por los humanos en los incendios y la hidrología, que causan la pérdida, degradación y fragmentación del hábitat, también son necesarios para asegurar que los esfuerzos de conservación enfocados en el clima no sean afectados por otras amenazas. Por lo tanto, los avances conceptuales y metodológicos para cuantificar los refugios potenciales ante múltiples factores estresantes causados por el humano son importantes para asegurar que los esfuerzos de conservación logren sus objetivos. Diseñamos una nueva estrategia conceptual, los dominios de los refugios, para evaluar la capacidad de refugio de un paisaje donde la exposición a múltiples factores estresantes es baja. En nuestro marco conceptual usamos los patrones de variabilidad ambiental (p. ej.: incremento en la frecuencia de veranos cálidos), los umbrales de resiliencia y la extensión e intensidad de los factores estresantes para identificar las áreas de refugios potenciales a partir de un conjunto de factores antropogénicos persistentes (p. ej.: cambios en el régimen de incendios). Para demostrar su utilidad, aplicamos el marco conceptual a un paisaje del sur de California. Los sitios con una alta capacidad de refugio (sitios de súper-refugios) tuvieron en promedio un 30% menos veranos extremadamente cálidos, 20% menos eventos de incendios y 50% menos senderos recreativos que el paisaje circundante. Nuestros resultados sugieren que los sitios de súper-refugios (∼ 8,200 km^2) para algunas comunidades naturales están subrepresentados en la red existente de áreas protegidas, un resultado que puede orientar los esfuerzos por expandir las áreas protegidas. Nuestro estudio de caso resalta que considerar la exposición a múltiples amenazas puede guiar la planificación y la práctica de la conservación de la biodiversidad en un mundo cambiante.

PALABRAS CLAVE:

biodiversity, climate change, global change, landscapes, Southern California, strategic planning and management, threats

【摘要】

从保护的角度来看，目前对潜在避难能力的量化主要关注的是气候避难所，它们对于维持物种和生态系统续存至关重要。然而，为了确保关注气候的保护工作不受其它威胁因素破坏，还需要考虑针对其它压力因素的保护，包括人类引起的火灾和水文变化，因为它们会导致栖息地丧失、退化和破碎化。因此，在概念和方法上推动量化多种人为压力因素的潜在避难所的研究进展，对支持保护工作十分重要。本研究设计了一个新的概念性方法 (即避难所领域) 用于评估避难能力，以识别受多种压力因素影响较小的地区。我们的框架利用环境变异性格局 (如暖夏出现频率增加)、恢复力阈值，以及压力因素的范围和强度来识别一系列持续的人为压力因素 (如火灾变化) 影响下的潜在避难所。为了证明该框架的有效性，我们将其应用于南加州的一处景观之中。结果表明，与周围景观相比，具有高避难能力的位点 (超级避难所) 极端暖夏出现的概率平均低 30%，火灾出现概率平均低 20%，河道和河岸地区被改变的风险低 10%，且存在的休闲步道少 50%。我们的结果指出，一些自然群落的超级避难所 (约 8,200 平方公里) 在现有的保护区网络中的代表性不足，这一发现可以指导扩大保护区的工作。我们的案例研究还强调了

考虑多种压力因素的暴露情况将如何为规划和实践提供信息，从而在不断变化的世界中保护生物多样性。
【翻译: 胡怡思; 审校: 聂永刚 】

关键词: 生物多样性, 威胁, 气候变化, 景观, 战略规划和管理, 全球变化, 南加州

INTRODUCTION

The specter of biodiversity loss due to human activities is widely recognized and well described in natural systems (Maxwell et al., 2016). Because of the ubiquity of these impacts, one central goal of biodiversity conservation has been to identify areas where the impacts can be mitigated, for example, reserves or sanctuaries (Rodrigues et al., 2004). In the context of rapid climate change, the term *refugia* describes habitats that provide spatial or temporal resistance or resilience (Morelli et al., 2020), where populations or subpopulations retreat to, persist in, and can potentially expand from under changing environmental conditions (Keppel et al., 2012, 2015). Although the terms *refugia* and *refuge* are used interchangeably (Selwood & Zimmer, 2020), and both terms can be used to refer to enclaves where suitable climate has allowed populations to persist over evolutionary timescales (Hampe & Jump, 2011; Stewart et al., 2010), we use *refugia* irrespective of the temporal scale of changes.

Although climate-change impacts are of mounting concern (e.g., Araújo et al., 2006; Scholze et al., 2006; Halsch et al., 2021), climate change is only one of many anthropogenic stressors contributing to biodiversity declines (Morris et al., 2020). Anthropogenic stressors also include altered disturbance regimes, habitat conversion and degradation, invasive species, pollution, and overexploitation (Maxwell et al., 2016). For example, too frequent fires can result in conversion of one vegetation physiognomic type to another (Syphard, Brennan, et al., 2019). Changes to hydrologic regimes, such as flooding and drought frequency and intensity, also negatively affect terrestrial and aquatic biodiversity (Kinoshita et al., 2016; McLaughlin et al., 2017). Although it is understood that multiple stressors drive biodiversity loss in concert, many studies continue to focus on the impacts of concurrent stressors independently (but see Grand et al., 2019).

The importance of a comprehensive evaluation of threats from multiple, synchronous stressors has been recognized and incorporated in several established conceptual approaches, such as novelty of ecosystems (Radeloff et al., 2015), indices of ecological integrity (McGarigal et al., 2018), the planetary boundaries framework (Steffen et al., 2015), and International Union for Conservation of Nature ecosystem risk assessments (Keith et al., 2013). The novelty of ecosystems concept explores the degree to which a site may experience novel biotic and abiotic conditions that have not previously been measured in space and time (Radeloff et al., 2015). The indices of ecological integrity focus on identifying land with the least direct impacts from human activities, such as roadless natural areas (McGarigal et al., 2018). The planetary boundaries framework estimates

thresholds at which human activities may disrupt key attributes of Earth systems, such as freshwater, biodiversity, and carbon storage (Rockstrom et al., 2009; Steffen et al., 2015). There is tremendous potential to integrate these and other frameworks that evaluate multiple anthropogenic stressors into local or regional conservation planning, particularly in the context of conserving dynamic landscapes (Jennings et al., 2020). Conservation planners typically evaluate patterns of land-use pressures to identify the most diverse and least fragmented areas for conservation at the lowest cost (Moilanen, 2007; Ball et al., 2009). Pairing these efforts with a comprehensive and spatially explicit assessment of multiple stressors beyond land-use change can effectively be used to maximize resilience of protected areas networks.

We devised a framework to quantify and visualize areas that have low exposure to multiple stressors, and thus higher refugial capacity (Keppel et al., 2015), that are more likely to facilitate persistence of species, populations, or communities in functional landscapes, and ultimately to identify superrefugia that can be targets of limited conservation resources. Although related to ecosystem risk assessments, the novelty of ecosystems, index of ecological integrity, and planetary boundary concepts, our refugial framework differs in scale (region vs. planet), focus (chronic and acute vs. novel stressors), and integration of both static and dynamic features of a landscape that influence refugial capacity. To consider multiple stressors, we integrated metrics of refugial capacity across different domains, which we define as social, ecological, or physical drivers, processes, or cycles that influence landscape structure, function, or composition. We used established metrics to quantify refugial conditions and considered how identifying refugial conditions across domains can inform conservation planning and management. Finally, we applied the domains of refugia concept to a biodiverse landscape in Southern California that has a range of anthropogenic stressors. We considered climate, fire, water, and human activity as our domains of interest.

FRAMEWORK OVERVIEW

The central idea that unifies the domains of refugia concept is the assumption that a refugium must help abate multiple stressors, not only climate change, thereby ensuring that a landscape can support species or population persistence (Figure 1). Using existing knowledge of landscape vulnerability, we focused on mapping refugia strictly from the perspective of exposure to multiple stressors that can cause biodiversity degradation at the landscape scale. We focused on 3 key and
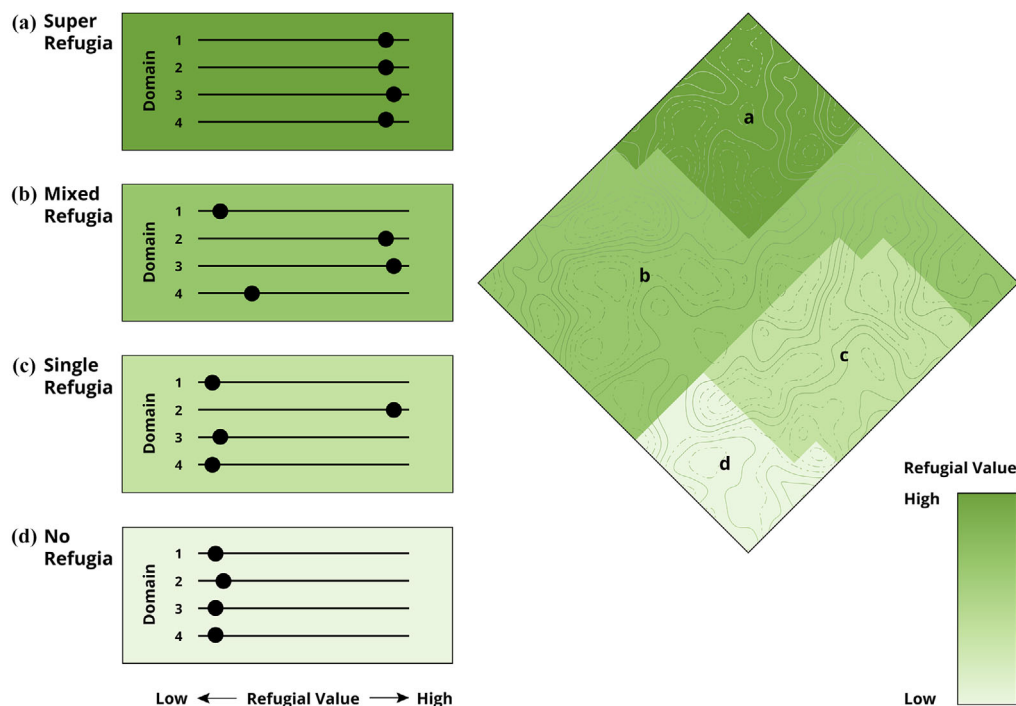
FIGURE 1 (a–d) Patterns of refugia created by spatial variability of exposure to multiple stressors across landscape domains (1–4), which are social, ecological, or physical drivers, processes, or cycles that exert influence on landscape structure, function, or composition. Figure design by Diane Terry, Climate Science Alliance.

generalizable questions: For what stressors do we need to map refugia to protect species and ecosystems in the region (Q1)? How can refugial conditions be quantified and mapped (Q2)? How can domains of refugia inform conservation planning and management (Q3)?

Stressors for which refugia are needed (Q1)

With our framework, we sought to quantify refugial capacity from multiple stressors across domains based on available data and information on species and natural communities. Some fairly ubiquitous stressors negatively affect biodiversity and ecosystem function globally (Maxwell et al., 2016). However, identifying which domains and stressors are relevant for a particular region should be based on the specific geography and ecology of the landscape and account for species and ecosystem vulnerability to anthropogenic stressors (Table 1).

Quantifying and mapping refugial conditions (Q2)

Determining appropriate metrics of refugial capacity can be based on measures of environmental stability, ecosystem resilience, and extent and intensity of threats. Environmental stability is a key concept often applied when describing refugia for species and ecosystem persistence or resistance to change (Keppel et al., 2015, Morelli et al., 2020) under current and

future climate change (McCullough et al., 2016). Although the biotic communities in a landscape may be adapted to shifting environmental conditions (Scheffer et al., 2001), the rate of change triggered by anthropogenic stressors can be too rapid for the community to respond and persist (Scholze et al., 2006). Consequently, refugia can be identified as locations that fall within a landscape's historical range of variability. This concept of environmental stability is the basis for metrics used to assess exposure to change, including magnitude (Ackerly et al., 2010), velocity (Loarie et al., 2009), and novelty of change (Radeloff et al., 2015). These metrics require the definition of a baseline, which can be set over an evolutionary time scale of hundreds of years or more (Radeloff et al., 2015), or an ecological timescale of 50 years, a common point for comparison to focus on exposure to recent environmental degradation (Keith et al., 2013; McCullough et al., 2016). Because patterns of environmental change vary among regions, conservation managers and practitioners should draw baselines from local analysis of their studied landscapes, specific to each domain, when information is available.

Refugial conditions may also be measured as a function of resilience as the maximum perturbation that an ecosystem can experience without a shift to an alternative state (Holling, 1973; Scheffer et al., 2001); the maximum perturbation represents a potential threshold. Thresholds can be determined by pairing baseline information on abiotic conditions with observations of system responses to disturbances that cause degradation (e.g., low river streamflow that causes tree death [Keith et al., 2013]) or by using statistical modeling approaches to identify drivers

TABLE 1 Typology for refugia from anthropogenic stressors that can alter ecosystem function and drive biodiversity loss.*

Domain	Category of exposure	Type of stressors
Climate change	Mean temperature	Displacement of average climatic conditions
		Climate velocity
		Novelty of climatic conditions
	Frequency and intensity of extreme events	Increase in warm temperatures
		Increase in number of heat waves
		Increase in frequency and length of droughts
	Precipitation	Decrease in snow versus liquid precipitation
	Sea level rise	Disappearance of coastal wetlands
	Altered cloud cover	Decrease in low cloud and fog thickness
Fire	Fire regime changes	Increase in fire frequency
		Increase in fire intensity and size
		Suppression of natural fires
		Loss of or decrease in unburned area within fire perimeter
Water	Hydrology and water quantity	Less basin recharge
		Increase in erosion and sedimentation
		Altered stream flow regime
		Increase in flood risk
		Increase in frequency and length of droughts
Human activities	Human use of wildlands	Increase in intensity of recreation activities
		Overexploitation of fauna
	Urban expansion	Spillover effect of invasive species into wildlands
		Pollution (e.g., increase light and noise)
		Loss of natural areas

Note: References are in Appendix S5. See table 4 in Keith et al. (2013) for a list of complementary variables to assess exposure to stressors.

that cause shifts to alternative states (Syphard, Brennan, et al., 2019).

When information about baselines or thresholds is limited, exposure can be quantified as the extent, intensity, and frequency of a stressor (McGarigal et al., 2018). Assessments of exposure can be extended to a formal risk analysis to estimate the possibility of degradation due to episodic hazards (e.g., risk of disease spread [Estrada- Peña et al., 2014] and exposure to chemicals and contaminants [Norton et al., 1992]).

Once identified and measured, metrics of exposure must be adjusted to a common scale to allow combining of refugia maps from multiple domains. Then, maps can be integrated, assuming an additive relationship among stressors, by weighting them equally. An alternative is to use weighting schemes to emphasize refugial capacity for different domains. Examples include weighting domains differently to account for the most proximate threat or according to management capacity or agency mandates. Regardless of which method is employed, it is important to compare weighting schemes with a baseline refugial capacity map, where all domains are weighted equally.

Using domains of refugia to inform conservation planning and management (Q3)

Once refugia have been delineated, they can inform existing conservation efforts. The framework is flexible in that it can be used to test hypotheses of differential impacts among stressors, through the use of weighting factors, as well as provide a means of comparing conservation outcomes under different climate scenarios. Identifying sites with high refugial capacity across the landscape may be important in prioritizing areas for restoration or management, buffer against uncertainty in the persistence of individual refugia, and support connectivity for species dispersal or migration based on spatial configuration of refugia. To identify priorities for land acquisition to expand or establish new protected areas, maps of refugial value can also be integrated into existing conservation planning approaches with a focus on climate change (Morelli et al., 2016) and traditional approaches of landscape conservation design (i.e., spatial optimization approaches that consider many factors, including costs, complementarity, redundancy, and connectivity [Moilanen, 2007; Ball et al., 2009]).

APPLYING DOMAINS OF REFUGIA TO A SOUTHERN CALIFORNIA LANDSCAPE

To demonstrate the framework, we applied the domains of refugia approach to a coastal landscape in Southern California, a hotspot of biodiversity that has lost more than half of its natural communities to development (Underwood et al., 2009) (Appendix S1).

Stressors for which refugia are needed (Q1)

To persist in the Southern California landscape, species and ecosystems may need refugia from shifting climatic conditions, including extremely hot summers and prolonged droughts (Cayan et al., 2010). In this landscape, changes in fire frequency can also be a significant stressor that can affect plant community structure and persistence (Syphard, Brennan, et al., 2019; Syphard, Rustigian-Romsos, et al., 2019). Furthermore, anthropogenic features that modify hydrologic flows alter the ability of watersheds to sustain functional habitats (Kinoshita et al., 2016). Finally, protected areas are often designed to mitigate the impacts of anthropogenic activities; however, recreational activities may alter the refugial capacity of the protected land, affecting the ability of the landscape to sustain species and their habitats (Larson et al., 2016).

Quantifying and mapping refugial conditions (Q2)

For each of the four domains, climate change, fire, water, and recreation, we identified associated anthropogenic stressors, accounting for existing knowledge of landscape vulnerability and availability of a wide diversity of data sources (Appendix S2). Below is an overview of the assumptions, approach, and findings for each of the metrics we used to measure refugial capacity (full description in Appendix S3).

We used two temperature metrics as proxies for climate change — the frequency of extreme summer temperatures and absolute change in mean summer maximum temperatures — using 90-m spatial resolution data of monthly maximum temperature from 1950 to 2019 (Flint et al., 2013). Assuming that less and slower change from past climate is an indicator of potential refugia (Loarie et al., 2009; Morelli et al., 2020), we calculated refugial capacity by comparing the recent past (1981–2019) with a historical baseline period (1950–1980). The threshold for extreme summer temperature was defined as the 90th percentile of maximum temperatures across all summer months (June, July, August, September) of the baseline period (Cayan et al., 2010). For each grid cell, we calculated the proportion that temperature above this baseline was observed in the recent past. To calculate the change in mean summer temperatures between the two periods, we averaged maximum temperatures of all summer months for each period. We considered exposure to drought in the water domain.

We used two metrics related to fire count to assess the refugial conditions of the fire domain. We used publicly available data from the Fire and Resource Assessment Program (2020). We generated a fire count from overlapping fire perimeters from 1878 to 2019 to identify sites that have historically burned at low frequency and may function as fire refugia. We also calculated the number of times each site (at the pixel level) met a threshold of a 15-year fire-return interval from 1950 to 2019 to identify sites less likely to experience vegetation-type conversion (Syphard, Brennan, et al., 2019). Our metrics of fire refugia are specific to our landscape, where increased fire frequency is the primary threat because it can degrade and convert natural communities. Further, although fire severity is important in many systems, in Southern California's chaparral, crown fires are typical and communities recover quickly (Keeley & Brennan, 2012). We considered fire separated from climate because ignition dynamics depend more on suburban development and are not directly aligned with climatic change (Syphard, Brennan, et al., 2019).

To evaluate the refugial condition of the water domain, we used a drought metric and the level of naturalness of the stream network. To assess exposure to prolonged periods of drought, we used the change in mean annual accumulated climatic water deficit between the baseline period (1950–1980) and the recent past (1981–2019). The climatic water deficit is an output of the Basin Characterization Model (Flint et al., 2013), constructed using climatic, soil, energy, and topographical conditions of a site. It provides a much more complete estimation of drought than other metrics that consider only precipitation (e.g., Standardized Precipitation Index). We combined this metric with the level of naturalness, amount of impervious surfaces or hardened rivers, a widely used metric representing the extent to which conversion of natural land cover has the potential to alter flows, reduce connectivity, or pollute water resources (Vörösmarty et al., 2010). To calculate stream naturalness, we assessed the proportion of natural land cover ∼30 m around the hydrological network (USGS, 2020) and aggregated the value at the watershed level.

To assess the impacts of human activities on refugial capacity, we used trail density to quantify exposure to recreational activities. Given the known impacts of recreational activities on a wide diversity of taxonomic groups (Larson et al., 2016), we assumed that areas with low trail density have the highest refugial capacity. To calculate trail density across our study area, we quantified kilometers of linear trail per square kilometer. We used data from OpenStreetMap Contributors (2020) and a 1-km search radius to detect trails of any length for each pixel of a 30-m-resolution map.

Mapping refugia across the landscape

To combine the metrics of refugia, we converted each of the data layers to a continuous raster surface with a unitless scale, ranging from 0 to 1, to evenly weight each metric:

$$X_{\text{rescaled}} = 1 - (X_i - X_{\text{min}})/X_{\text{range}}, \quad (1)$$

where X_i is the value at grid cell i and X_{min} and X_{range} are the minimum value and the range, respectively, for each variable at its original scale (higher values indicate areas of higher refugial capacity). For domains with multiple metrics, we converted each layer based on a relative scale, added the layers within the domain, and then rescaled the combined layers. To identify areas of refugia across multiple domains, we summed, using equal weights, the rescaled values from each map. We also tested two user-defined weighting schemes to consider the impacts of differential weighting among domains, reflecting the importance of the two most pressing stressors in our landscape. In each test, we doubled the weight of fire and then recreation relative to the other domains. In future applications, end users may want to test different weight assignments to evaluate the effects on the final refugia map. We used Pearson's index to assess correlation between refugial maps.

Spatial distribution and size of super-refugia (Q3)

Once we evaluated refugial conditions across domains, we selected a portion of the study area with the highest refugial values, defined as super-refugia. To identify priorities for conservation planning and implementation of management actions, we assessed connectivity by evaluating the distribution of sizes of super-refugia sites and average distance between them. In addition, we calculated Euclidean distance among the three largest sites. We assessed the protection status of the refugia sites by evaluating the extent to which they occur in conserved lands. Finally, we quantified the diversity of natural communities in super-refugia sites to assess the extent to which current conserved lands provide protection to underrepresented natural communities.

RESULTS

We found differences in the spatial distribution of refugia across domains (Figure 2b–e). On the one hand, we found little overlap between fire that often occurred at higher elevations and climate refugia located at lower elevations. On the other hand, we found evidence of spatial overlap between areas of recreation and water refugia. Overall, we found our metrics were complementary because there were no strong correlations among domains (Appendix S4).

Average refugial capacity was 3.06 and ranged from 1.92 to 3.68 (out of maximum of 4), demonstrating that all sites had some refugial value for some domains. The 30% of the study area that had the highest refugial values (average 3.3, range 3.18–3.68) encompassed approximately 8200 km^2. In these super-refugia, exposure was characterized as having 30% fewer extremely warm summer months, 20% fewer fire events, 10% less exposure to altered river channels and riparian areas, and 50% fewer recreational trails per unit area than the rest of the landscape (Appendix S4).

More than half of the super-refugia sites (60%, 4900 km^2) were encompassed in existing conserved lands (Figure 3a) that included more than 30 natural communities (Appendix S4). The vast majority were chaparral communities (~54%, 4400 km^2), indicating that the dominant natural community in the study region is well represented in conserved land (>70% is currently protected). A smaller percentage of the super-refugia sites (~19%) support more sparsely represented communities, including annual grassland, oak woodland, and coastal sage scrub. Less than 40% of their area was conserved. In terms of spatial distribution, we found one large super-refugia site (1800 km^2) in the northern region and two large areas (1300–3300 km^2) in the southern portion of the study area (Figure 3b). Between these large refugia, we identified a substantial number (>840) of small (1–10 km^2) refugia sites distributed across the landscape, some of which were in conserved lands adjacent to developed areas (Figure 3c,d). Although a considerable distance (~180 km) and a region of dense urbanization separated the two largest refugia sites, we found an average nearest neighbor distance of 1.3 km between refugia sites of all sizes.

DISCUSSION

One of the central principles of conservation planning is that stressors must be abated to meet conservation targets (Rodrigues et al., 2004; Keith et al., 2013). However, to do so requires an ability to identify and quantify the multiple, synchronous stressors in a given region (Keith et al., 2013; Morris et al., 2020). The domains of refugia framework provides a flexible approach that can be used to identify stressors that are known to affect species and ecosystem functioning, select metrics to assess exposure based on a diversity of approaches to account for knowledge and data availability, and map potential refugial conditions. Identifying sites with refugial capacity can inform conservation efforts to assess the degradation status of global ecosystems (Keith et al., 2013), and it can guide landscape conservation planning (e.g., Moilanen, 2007).

Implications for conservation planning and practice

One of the primary applications of the domains of refugia framework is to improve and strengthen conservation planning. Our finding that a relatively small portion of the existing conserved land (~30%) in Southern California has refugial capacity from the most prevalent landscape stressors suggests that prior conservation planning efforts have not explicitly included a comprehensive evaluation of stressors, a finding not unique to Southern California (Keith et al., 2013). Encouragingly, we found that a high proportion (60%) of the refugia sites occur in existing protected areas, which suggests that expanding protected areas to include additional refugia areas is feasible. We also identified refugia not currently in conserved land where underrepresented ecosystems, such as
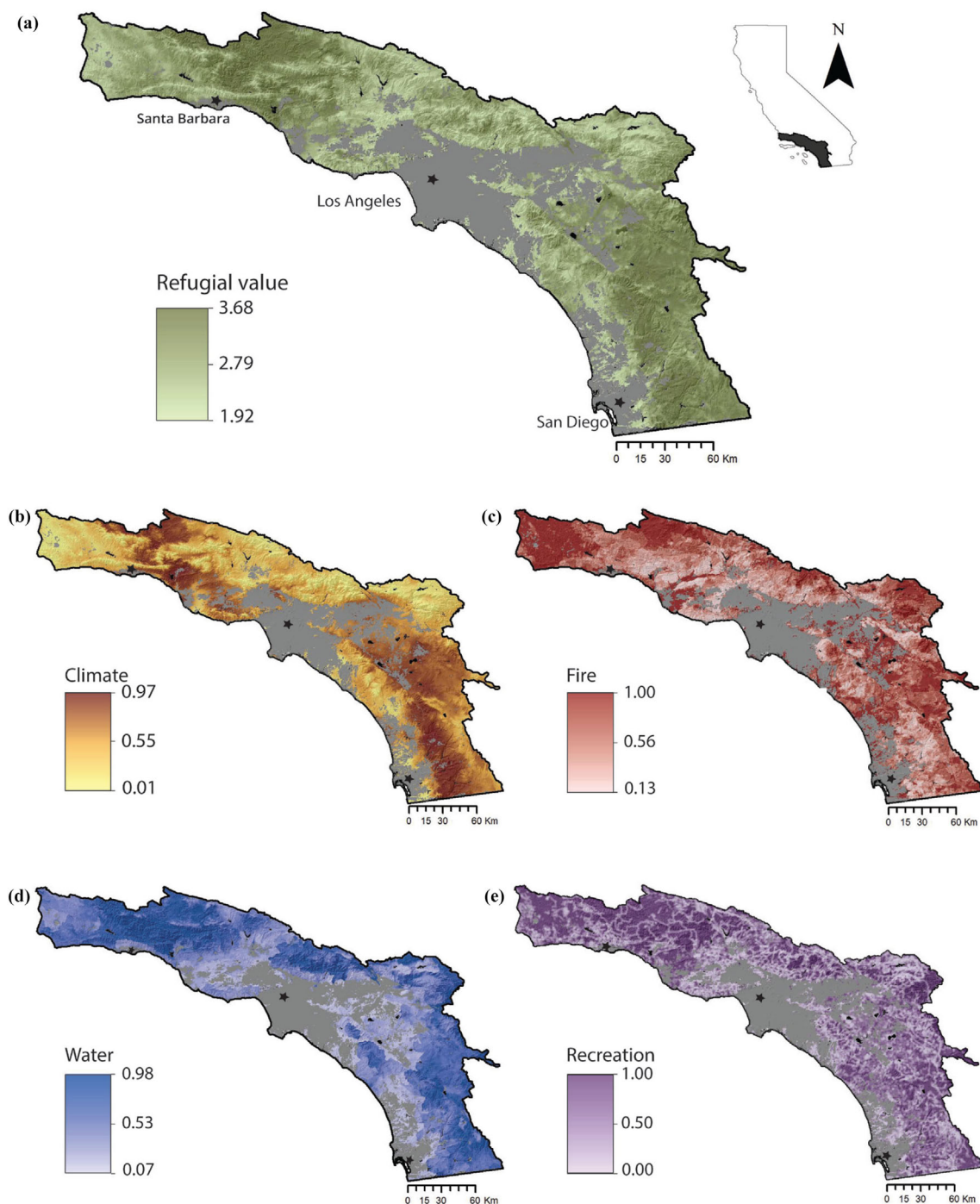
FIGURE 2 In Southern California (USA), gradient of (a) overall refugial capacity and refugia related to the domains of (b) climate, (c) fire, (d) water, and (e) recreation (gray, masked urban areas). The single-domain refugia maps are based on a combination of multiple or single metrics of exposure to conditions that can generate stress in each domain (see Appendix S3 for more information)

grassland, oak woodland, and coastal scrub, could be protected (Underwood et al., 2009). Likewise, our analyses of the size and spatial distribution of super-refugia highlighted important targets for acquisition and management to protect refugial capacity. Although these largest refugia sites are separated by >180 km, there were a large number of small refugia in relatively close proximity (1.3 km) that may serve as stepping stones, facilitat-

ing movement among refugia sites (Hannah et al., 2014). The fact that we did not find strong relationships among domains also suggests that having less exposure to one stressor does not necessarily afford protection from others. For instance, fire and climate refugia were located in geographically distinct regions; high fire exposure was at low elevations and high climate exposure at high elevations, consistent with results of previous
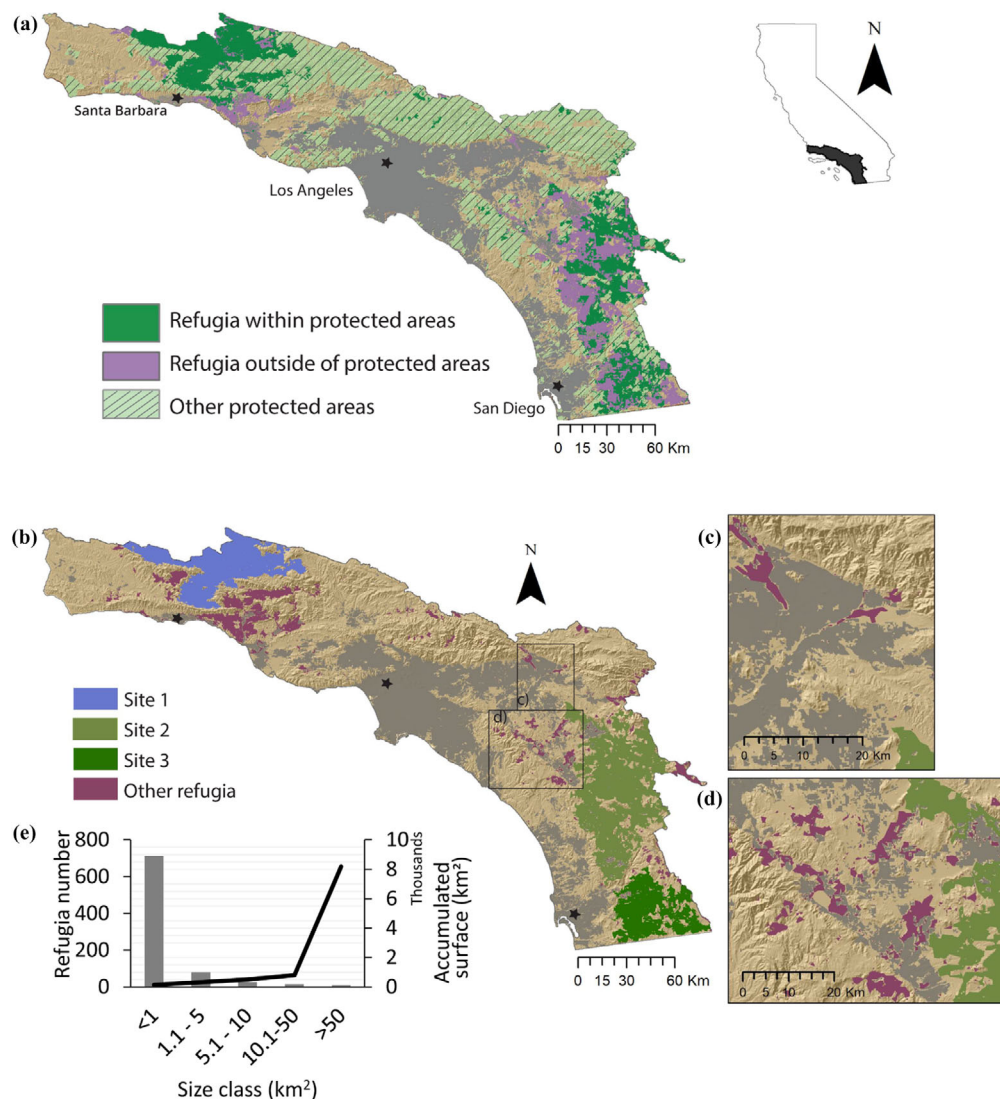
FIGURE 3 (a) Overlap of super-refugia sites inside (green) and outside (purple) protected areas (hatching, protected areas that do not have high refugial capacity). (b) Three largest refugia sites, (c and d) smaller refugia sites clustered around the largest sites, and (e) distribution of the number of refugia by size class and total area of super-refugia across the study region (gray, urban areas)

studies (McCullough et al., 2016; Syphard, Brennan, et al., 2019; Syphard, Rustigian-Romsos, et al., 2019).

Refining and expanding the refugia framework

For our demonstration, we adopted an approach focused on landscape-scale vulnerabilities to ubiquitous stressors rather than individual species characteristics, in part because of the knowledge gaps on the effects of many stressors on particular conservation targets, such as threatened or endangered species. Future applications of the concept could incorporate adaptive capacity or vulnerability of individual species or populations to consider these biological effects of exposure to stress, with finer-scale conservation targets in mind (Foden et al., 2019). For some applications, generating a refugia map for a particu-lar species, assemblage, or natural community may be useful in identifying both current and likely future refugia from a range of stressors.

Another important consideration for future applications of our framework is the synergistic effects of stressors. In our demonstration, we assumed an additive relationship among stressors. However, interactions among stressors may take multiple forms (Côté et al., 2016). For example, interactions between fire and drought can lead to increases in exotic species, creating a feedback loop that increases the impact of these stressors over time (Keeley & Brennan, 2012). Furthermore, a natural extension of our work is to use future projections and scenarios of global change to consider potential displacement and reduction of refugial capacity over time. Such an approach has been applied frequently in climate-change assessments (e.g., Hannah et al., 2014). Our approach could be expanded to

include projections and scenarios of land use, fire, and hydrology (Flint et al., 2013).

We used established metrics of exposure used previously in our study area (McCullough et al., 2016) to reflect existing conditions and to better account for uncertainty (Appendix S3). Future users of our approach may expand to other metrics that provide a measure of significance and variability in the mean condition, such as trend analysis. Approaches to deal with uncertainty in applications of future scenarios of change include averaging conditions across scenarios, using two scenarios that provide the two extremes (minimum and maximum), or choosing scenarios that align well relative to recent observations.

One of the primary strengths of the domains of refugia framework is that it is transferable to different landscapes and can be readily adapted for a variety of purposes because it can be used to identify, quantify, and integrate regionally relevant stressors. Our approach emphasizes the importance of considering the multiple domains that affect landscapes to advance proactive conservation. In particular, the ability to identify areas of high refugial capacity can guide decisions regarding land acquisition, restoration, or other management activities and ultimately meet conservation objectives for dynamic landscapes (Jennings et al., 2020).

ACKNOWLEDGMENTS

ORCID

Isabel M. Rojas https://orcid.org/0000-0002-4255-3768
Megan K. Jennings https://orcid.org/0000-0002-3707-851X
Erin Conlisk https://orcid.org/0000-0002-4049-4805
Alexandra D. Syphard https://orcid.org/0000-0003-3070-0596
Alicia M. Kinoshita https://orcid.org/0000-0002-2283-4490
Doug Stow https://orcid.org/0000-0001-5246-7073
Emanuel Storey https://orcid.org/0000-0001-8896-1444
Mark E. De Guzman https://orcid.org/0000-0002-3393-8084
Sherry Ryan https://orcid.org/0000-0002-9839-9958
Lorraine E. Flint https://orcid.org/0000-0002-7868-441X
Alan L. Flint https://orcid.org/0000-0002-5118-751X
Rebecca L. Lewison https://orcid.org/0000-0003-3065-2926

LITERATURE CITED

Ackerly, D. D., Loarie, S. R., Cornwell, W. K., Weiss, S. B., Hamilton, H., Branciforte, R., & Kraft, N. J. (2010). The geography of climate change: Implications for conservation biogeography. *Diversity and Distributions*, 16(3), 476–487.

Araújo, M. B., Thuiller, W., & Pearson, R. G. (2006). Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, 33(10), 1712–1728.

Ball, I. R., Possingham, H. P., & Watts, M. (2009). Marxan and relatives: Software for spatial conservation prioritization. In A. Moilanen, K. A. Wilson, & H. P. Possingham (Eds.), *Spatial conservation prioritization: Quantitative methods and computational tools* (pp. 185–195). Oxford University Press.

Cayan, D. R., Das, T., Pierce, D. W., Barnett, T. P., Tyree, M., & Gershunova, A. (2010). Future dryness in the Southwest US and the hydrology of the early 21st century drought. *Proceedings of the National Academy of Sciences of the United States of America*, 107(50), 21271–21276.

Côté, I. M., Darling, E. S., & Brown, C. J. (2016). Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, 283(1824), 20152592.

Estrada-Peña, A., Ostfeld, R. S., Peterson, A. T., Poulin, R., & de la Fuente, J. (2014). Effects of environmental change on zoonotic disease risk: An ecological primer. *Trends in Parasitology*, 30(4), 205–214.

Flint, L. E., Flint, A. L., Thorne, J. H., & Boynton, R. (2013). Fine-scale hydrologic modeling for regional landscape applications: The California Basin Characterization Model development and performance. *Ecological Processes*, 2, 25.

Foden, W. B., Young, B. E., Akçakaya, H. R., Garcia, R. A., Hoffmann, A. A., Stein, B. A., Thomas, C. D., Wheatley, C. J., Bickford, D., Carr, J. A., Hole, D. G., Martin, T. G., Pacifici, M., Pearce-Higgins, J. W., Platts, P. J., Visconti, P., Watson, J. E. M., & Huntley, B. (2019). Climate change vulnerability assessment of species. *Climate Change*, 10(1), 1–36.

Grand, J., Wilsey, C., Wu, J. X., & Michel, N. L. (2019). The future of North American grassland birds: Incorporating persistent and emergent threats into full annual cycle conservation priorities. *Conservation Science and Practice*, 1, e20.

Halsch, C. A., Shapiro, A. M., Fordyce, J. A., Nice, C. C., Thorne, J. H., Waetjen, D. P., & Forister, M. L. (2021). Insects and recent climate change. *Proceedings of the National Academy of Sciences*, 118(2), e2002543117.

Hampe, A., & Jump, A. S. (2011). Climate relics: Past, present, future. *Annual Review of Ecology, Evolution, and Systematics*, 42(1), 313–333.

Hannah, L., Flint, L., Syphard, A. D., Moritz, M. A., Buckley, L. B., & McCullough, I. M. (2014). Fine-grain modeling of species' response to climate change: Holdouts, stepping-stone, and microrefugia. *Trends in Ecology & Evolution*, 29(7), 390–397.

Holling, C. S. (1973). Resilience and stability of ecological systems. *Annual Review in Ecology, Evolution and Systematics*, 4, 1–23.

Jennings, M. K., Haeuser, E., Foote, D., Lewison, R. L., & Conlisk, E. (2020). Planning for dynamic connectivity: Operationalizing robust decision-making and prioritizing across landscapes experiencing climate and land-use change. *Land*, 9(10), 341.

Keeley, J. E., & Brennan, T. J. (2012). Fire-driven alien invasion in a fire-adapted ecosystem. *Oecologia*, 169(4), 1043–1052.

Keith, D. A., Rodríguez, J. P., Rodriguez-Clark, K., Nicholson, E., Aapala, K., Alonso, A., Asmussen, M., Bachman, S., Basset, A., Barrow, E. G., Benson, J. S., Bishop, M. J., Bonifacio, R., Brooks, T. M., Fairweather, P. G., Holdaway, R. J., Jennings, M., Kingsford, R. T., Lester, R. E., … Zambrano-marti, S. (2013). Scientific foundations for an IUCN Red List of ecosystems. *PLoS ONE*, 8(5), e62111.

Keppel, G., Van Niel, K. P., Wardell-Johnson, G. W., Yates, C. J., Byrne, M., Mucina, L., Schut, A. G. T., Hopper, S. D., & Franklin, S. E. (2012). Refugia: Identifying and understanding safe havens for biodiversity under climate change. *Global Ecology and Biogeography*, 21, 393–404.

Keppel, G., Mokany, K., Wardell-Johnson, G. W., Phillips, B. L., Welbergen, J. A. & Reside, A. E. (2015). The capacity of refugia for conservation planning under climate change. *Frontiers in Ecology and the Environment*, 13(2), 106–112.

Kinoshita, A. M., Chin, A., Simon, G. L., Briles, C., Hogue, T. S., O'Dowd, A. P., Gerlak, A. K., & Uribe, A. (2016). Wildfire, water, and society: Toward integrative research in the "Anthropocene". *Anthropocene*, *16*, 16–27.

Larson, C. L., Reed, S. E., Merenlender, A. M., & Crooks, K. R. (2016). Effects of recreation on animals revealed as widespread through a global systematic review. *PLoS ONE*, *11*(12), e0167259.

Loarie, S. R., Duffy, P. B., Hamilton, H., Asner, G. P., Field, C. B., & Ackerly, D. D. (2009). The velocity of climate change. *Nature*, *462*(7276), 1052–1055.

Maxwell, S. L., Fuller, R. A., Brooks, T. M., & Watson, J. E. M. (2016). The ravages of guns, nets and bulldozers. *Nature*, *536*, 143–145.

McCullough, I. M., Davis, F. W., Dingman, J. R., Flint, L. E., Flint, A. L., Serra-Diaz, J. M., Syphard, A. D., Moritz, M. A., Hannah, L., & Franklin, J. (2016). High and dry: High elevations disproportionately exposed to regional climate change in Mediterranean-climate landscapes. *Landscape Ecology*, *31*(5), 1063–1075.

McGarigal, K., Compton, B. W., Plunkett, E. B., DeLuca, W. V., Grand, J., Ene, E., & Jackson, S. D. (2018). A landscape index of ecological integrity to inform landscape conservation. *Landscape Ecology*, *33*(7), 1029–1048.

McLaughlin, B. C., Ackerly, D. D., Klos, P. Z., Natali, J., Dawson, T. E., & Thompson, S. E. (2017). Hydrologic refugia, plants, and climate change. *Global Change Biology*, *23*(8), 2941–2961.

Moilanen, A. (2007). Landscape Zonation, benefit functions and target-based planning: Unifying reserve selection strategies. *Biological Conservation*, *134*(4), 571–579.

Morelli, T. L., Daly, C., Dobrowski, S. Z., Dulen, D. M., Ebersole, J. L., Jackson, S. T., Lundquist, J. D., Millar, C. I., Maher, S. P., Monahan, W. B., Nydick, K. R., Redmond, K. T., Sawyer, S. C., Stock, S., & Beissinger, S. R. (2016). Managing climate change refugia for climate adaptation. *PLoS ONE*, *11*(8), e0159909.

Morelli, T. L., Barrows, C. W., Ramirez, A. R., Cartwright, J. M., Ackerly, D. D., Eaves, T. D., Ebersole, J. L., Krawchuk, M. A., Letcher, B. H., Mahalovich, M. F., Meigs, G. W., Michalak, J. L., Millar, C. I., Quiñones, R., Stralberg, D., & Thorne, J. H. (2020). Change refugia: Biodiversity in the slow lane. *Frontiers in Ecology and the Environment*, *18*(5), 228–234.

Morris, W. F., Ehrlén, J., Dahlgren, J. P., Loomis, A. K., & Louthan, A. M. (2020). Biotic and anthropogenic forces rival climatic/abiotic factors in determining global plant population growth and fitness. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(2), 1107–1112.

Norton, S. B., Rodier, D. J., van der Schalie, W. H., Wood, W. P., Slimak, M. W., & Gentile, J. H. (1992). A framework for ecological risk assessment at the EPA. *Environmental Toxicology and Chemistry*, *11*(12), 1663–1672.

Radeloff, V. C., Williams, J. W., Bateman, B. L., Burke, K. D., Carter, S. K., Childress, E. S., Cromwell, K. J., Gratton, C., Hasley, A. O., Kraemer, B. M., Latzka, A. W., Marin-Spiotta, E., Meine, C. D., Munoz, S. E., Neeson, T. M., Pidgeon, A. M., Rissman, A. R., Rivera, R. J., Szymanski, L. M., & Usinowicz, J. (2015). The rise of novelty in ecosystems. *Ecological Applications*, *25*(8), 2051–2068.

Rockström, J., Steffen, W., Noone, K., Persson, Å., Chapin, F. S., III, Lambin, E., Lenton, T. M., Scheffer, M., Folke, C., Schellnhuber, H., Nykvist, B., De Wit, C. A., Hughes, T., van der Leeuw, S., Rodhe, H., Sörlin, S., Snyder, P. K., Costanza, R., Svedin, U., … Foley, J. (2009). Planetary boundaries: Exploring the safe operating space for humanity. *Ecology and Society*, *14*(2), 32.

Rodrigues, A. S. L., Andelman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., Fishpool, L. D. C., Da Fonseca, G. A., Gaston, K. J., Hoffmann, M., Long, J. S., Marquet, P. A., Pilgrim, J., Pressey, R., Schipper, J., Sechrest, W., Stuart, S. N., Underhill, L. G., Waller, R. W., … Yan, X. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature*, *428*(6983), 640–643.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, *413*, 591–596.

Scholze, M., Knorr, W., Arnell, N. W., & Prentice, I. C. (2006). A climate-change risk analysis for world ecosystems. *Proceeding of the National Academy of Sciences of the United State of America*, *103*(35), 13116–13120.

Selwood, K. E., & Zimmer, H. C. (2020). Refuges for biodiversity conservation: A review of the evidence. *Biological Conservation*, *245*, e108502. https://doi.org/10.1016/j.biocon.2020.108502

Steffen, W., Richardson, K., Rockström, J., Cornell, S. E., Fetzer, I., Bennett, E. M., Biggs, R., Carpenter, S. R., De Vries, W., De Wit, C. A., Folke, C., Gerten, D., Heinke, J., Mace, G. M., Persson, L. M., Ramanathan, V., Reyers, B., & Sörlin, S. (2015). Planetary boundaries: Guiding changing planet. *Science*, *347*(6223). https://doi.org/10.1126/science.1259855

Stewart, J. R., Lister, A. M., Barnes, I., & Dalén, L. (2010). Refugia revisited: Individualistic responses of species in space and time. *Proceedings of the Royal Society B: Biological Sciences*, *277*(1682), 661–671.

Syphard, A., Brennan, T., & Keeley, J. (2019). Drivers of chaparral type conversion to herbaceous vegetation in coastal Southern California. *Diversity and Distributions*, *25*(1), 90–101.

Syphard, A. D., Rustigian-Romsos, H., Mann, M., Conlisk, E., Moritz, M. A., & Ackerly, D. (2019). The relative influence of climate and housing development on current and projected future fire patterns and structure loss across three California landscapes. *Global Environmental Change*, *56*, 41–55.

Underwood, E. C., Viers, J. H., Klausmeyer, K. R., Cox, R. L., & Shaw, M. R. (2009). Threats and biodiversity in the mediterranean biome. *Diversity and Distributions*, *15*(2), 188–197.

United States Geological Survey (USGS). (2020). *National Hydrography Dataset V2.3.* https://www.usgs.gov/core-science-systems/ngp/national-hydrography

Vörösmarty, C. J., McIntyre, P. B., Gessner, M. O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S. E., Sullivan, C. A., Liermann, C. R., & Davies, P. M. (2010). Global threats to human water security and river biodiversity. *Nature*, *467*(7315), 555–561.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.