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Exposure of protected areas in Central America to extreme weather events

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Abstract

Central America and the Caribbean are regularly battered by megadroughts, heavy rainfall, heat waves, and tropical cyclones. Although 21st-century climate change is expected to increase the frequency, intensity, and duration of these extreme weather events (EWEs), their incidence in regional protected areas (PAs) remains poorly explored. We examined historical and projected EWEs across the region based on 32 metrics that describe distinct dimensions (i.e., intensity, duration, and frequency) of heat waves, cyclones, droughts, and rainfall and compared trends in PAs with trends in unprotected lands. From the early 21st century onward, exposure to EWEs increased across the region, and PAs were predicted to be more exposed to climate extremes than unprotected areas (as shown by autoregressive model coefficients at p < 0.05 significance level). This was particularly true for heat waves, which were projected to have a significantly higher average (tested by Wilcoxon tests at p < 0.01) intensity and duration, and tropical cyclones, which affected PAs more severely in carbon-intensive scenarios. PAs were also predicted to be significantly less exposed to droughts and heavy rainfall than unprotected areas (tested by Wilcoxon tests at p < 0.01). However, droughts that could threaten connectivity between PAs are increasingly common in this region. We estimated that approximately 65% of the study area will experience at least one drought episode that is more intense and longer lasting than previous droughts. Collectively, our results highlight that new conservation strategies adapted to threats associated with EWEs need to be tailored and implemented promptly. Unless urgent action is taken, significant damage may be inflicted on the unique biodiversity of the region.

KEYWORDS

climate adaptation, climate change, climate exposure, conservation planning, droughts heavy rainfall, hurricanes, restoration

INTRODUCTION

Despite widespread recognition of climate change effects on biodiversity (Pecl et al., 2017; Pereira et al., 2012), the impacts of extreme weather events (EWEs) have received limited attention. Yet, compared with gradual climate changes, EWEs can have more devastating effects (Harris et al., 2018; Sabater et al., 2022; Wethey et al., 2011). Disruption of species' life cycles, local population collapses, habitat loss, connectivity disruptions, and community disassembly are just some of the consequences of EWEs (Buckley & Huey 2016; França et al., 2020; GonzálezTrujillo et al., 2023; Kreyling et al., 2014; Smale & Wernberg 2013). Understanding the historical and future trajectories of EWEs is thus critical for effective biodiversity conservation planning in the face of climate change.

Regions near the equator, including Central America, Africa, and South Asia, are particularly exposed to a combination of several forms of extreme climate changes (Garcia et al., 2014; Thompson et al., 2023). Central America and the Caribbean region are notoriously affected by EWEs, such as heat waves, heavy rainfall, droughts, and tropical cyclones (Cook et al., 2022; Reyer et al., 2017; Taylor et al., 2012). The impact of these

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events on the region's unique biodiversity has not been extensively studied, but several projections indicate that the intensity, frequency, and duration of EWEs will increase in the future (Avila-Diaz et al., 2023; Castellanos et al., 2022). However, some important questions remain: would protected areas (PAs) be well placed to act as buffers against the effects of EWEs on biodiversity; would they be disproportionately exposed to them; and are there areas in Central America and the Caribbean projected to be consistently overexposed or underexposed to EWEs? In other words, can areas that will require greater protection from EWEs in the future and areas that could serve as climate refugia be identified?

We quantified the exposure of Mesoamerican and Caribbean PAs to historical (observed) and future (projected) EWEs. EWEs can be characterized by metrics describing their intensity, frequency, duration, or interactions among these 3 dimensions. In addition, they can focus on different climate variables, such as high temperatures (heat waves), peaks and shortages of precipitation (heavy rainfall and droughts, respectively), and strong wind speeds (tropical cyclones). Using climate metrics characterizing 4 dimensions and 4 variables across dry and wet seasons, we asked whether exposure to EWEs is more pronounced in PAs or across unprotected territory. We used historical daily time series, projections of future climate change, and 3 socioeconomic scenarios (IPCC, 2021) to answer this question. We then quantified overexposure to EWEs in the future to identify areas with low and high probabilities of exposure to EWEs in the next 70 years. Finally, we mapped regional patterns of the lowest overexposure-to-EWEs scores to help identify regions potentially suitable for PA expansion, conservation, or restoration.

METHODS

Climatic data

We investigated changes in exposure to EWEs from 1952 until 2100 with gridded data on temperature, wind speed, and precipitation with a daily temporal resolution and a spatial resolution of $0.5^{\circ} \times 0.5^{\circ}$. Climatic data were retrieved from the ISIMIP portal (https://data.isimip.org, accessed on 10 January 2023), which contains downscaled and bias-adjusted climatic data (method ISIMIP3BASD 2.5 [Lange et al., 2020]) generated using different CMIP6 models. To compute metrics, we used daily values obtained by the GFDL-ESM4 model under 3 shared socioeconomic pathways (SSPs) (SSP126, SSP370, and SSP585) (IPCC, 2021). This model was chosen because of its reliability to reproduce extreme values (Chen et al., 2020). In SSP126 (sustainability scenario), the world gradually and extensively shifts toward a more sustainable path. In SSP370 (regional rivalry scenario), countries prioritize the achievement of climatic security in their own regions even if it comes at the expense of broader-based development. In SSP585 (fossil-fueled development), global progress heavily depends on fossil fuels, leading to high emissions that result in a radiative forcing of 8.5 W/m² by 2100.

Metrics of exposure

A wide array of metrics exists to describe the multiple dimensions of EWEs (González-Trujillo et al., 2023). Metrics can be used to describe an EWE in terms of its unusual frequency, intensity, or duration and be based on different sets of variables, such as temperature, precipitation, and wind speed. We calculated the intensity, frequency, duration, and interaction between intensity and duration (4 dimensions) of heat waves (i.e., temperature driven), meteorological droughts (i.e., precipitation driven), heavy rainfall (i.e., precipitation driven), and tropical cyclones (i.e., driven by wind speed) (4 climatic variables) (Table 1). Metrics were computed separately in $0.5^{\circ} \times 0.5^{\circ}$ grid cells for the dry season (i.e., December to April) and the wet season (i.e., June to October) (Table 1). This resulted in 32 metrics (4 dimensions, 4 climatic variables, and 2 seasons) describing exposure to EWEs across the Caribbean and Central America from 1952 to 2100 under the 3 SSPs. Data and dynamic representations of exposure metrics are available at GitHub (https:// github.com/jdgonzalezt/extremeEventsProtectedAreas).

Protected areas

PA boundaries were obtained from the WDPA database (https://www.protectedplanet.net/en/thematic-areas/wdpa? tab=WDPA, accessed on 10 March 2023). We included PAs classified as IUCN (International Union for Conservation of Nature) management categories I–VI and areas with no assigned management category because these may still offer reasonably high levels of protection. The shapefile was clipped to the landmass of the Central America continent and the Caribbean islands, based on the Global Administrative Areas Database (http://gadm.org), so as to keep the terrestrial component of coastal PAs. PA shapefiles were merged using ArcGIS 10.2.

To establish a binary classification of protected and unprotected grid cells, and following Araújo (2004), we tested a full range of thresholds (i.e., percentage grid cell area protected), from 0% to 100% (at a decimal basis), and chose the one that best approximated the total area of the protected grid cells to the total area covered with PAs in the region (i.e., a 40.9% threshold for PAs in a grid cell) (Appendix S1). Because the region has several small PAs scattered within the grid cell mesh, we also examined patterns obtained using a 20% PA threshold. This analysis enabled us to quantify exposure of EWE on smaller PAs. Herein, we present results derived from the 40.9% threshold (henceforth referred to as 41%), but they were qualitatively similar to those obtained using the 20% threshold (Appendix S2).

Statistical analyses

Unless specifically stated otherwise, all modeling processes were conducted using R 4.2.1 (R Core Team, 2022). The analyses included all protected and unprotected grid cells in the study

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TABLE 1 Climate metrics used to measure the multiple dimensions of extreme weather events.

Dimension	Metric (abbreviation)	Description	References
Intensity	Number of extreme standardized anomalies (nSA)	Number of standardized anomalies above 3 SD computed using maximum or minimum (in the case of meteorological droughts) daily values in a season or year	González-Trujillo et al., 2023
Intensity and duration	Cumulative intensity of persistent climate extremes (MCI)	Cumulative mean of the excess magnitude of any climatic variable linearly weighted by the duration of the event; persistent event (PE) defined as 5 or more consecutive days where the daily maximum is above or daily minimum is below (in the case of meteorological droughts) the established threshold (P95th or P5th)	Perkins & Alexander, 2013
Duration	Duration of persistent climate extremes (MRT)	Median number of consecutive days per season or year where the daily maximum (or minimum in the case of meteorological droughts) is above or daily minimum is below the established baseline (P95th or P5th)	Sillmann et al., 2013
Frequency	Persistent climate extremes (PE)	Number of events in which daily maximum is above, or daily minimum is below (in the case of meteorological droughts), the established threshold (P95th or P5th) for 5 or more consecutive days	Buckley & Huey, 2016

Abbreviations: MCI, mean cumulative intensity; MRT, mean residency time; nSA, number of standardized anomalies above 3 SD; P5th, 5th percentile; P95th, 95th percentile.

window. Spatial data sets were reprojected to conform to the WGS84 projection system.

We used a spatial autocorrelation modeling framework (Ver Hoef et al., 2018) to investigate whether exposure to EWEs differed between protected and unprotected areas on an annual basis. First, we calculated the isotropic semivariograms for each metric, variable, season, and PAs to determine the geographical extent of the autocorrelation signals. We used the variogram function from the gstat R package (Gräler et al., 2016) to fit an exponential model that best fitted the empirical values of all cases. Neighborhood weights for each grid cell were then determined based on autocorrelation ranges. Spatial lag vectors were derived for each variable, metric, season, and PA with the lag.listw function of the spdep R package (Bivand, 2022).

Linear regression models were formulated with each variable \times indicator \times season as the dependent variable and the lag vector and an indicator variable discriminating between protected and unprotected grid cells as predictors. The coefficients associated with the indicator variables indicate the average relative exposure in PAs compared with unprotected areas. We controlled for the structure of spatial autocorrelation. Thus, a coefficient significantly different from zero (p < 0.05) indicated that exposure to EWEs was higher (for positive coefficients) or lower (for negative coefficients) in PAs compared with unprotected grid cells. We built linear models by merging the normalized scores of the 32 metrics. Given that the different metrics were measured using distinct units, to ensure consistency, the data for each metric and year were standardized from zero to one. We ran additional models for the combination of each climatic variable and season independently.

We conducted a complementary analysis with the Wilcoxon rank-sum test to compare historical and future values for each metric inside and outside PAs. For both periods (historical, 1952–2016; future, 2016–2100) and for each of the 32 EWE metrics, the Wilcoxon test was performed using the R function wilcox.test to determine whether the distribution of exposure values differed significantly between protected and unprotected grid cells (significance level p < 0.01). Additionally, we computed the Cliff's delta (Cliff, 1993) effect size to determine the magnitude and direction of the differences. Cliff's delta estimates the probability that a value selected from one of the groups being compared is greater than a value selected from the other group. It varies from -1 to +1; values farther from zero indicate the absence of overlap between the 2 groups. In our analyses, negative values indicated that unprotected cells had greater exposure to extreme climate than protected cells, whereas positive values indicated the opposite. Cliff's delta was calculated using the cliff.delta function of the effsize R package (Torchiano, 2020).

To quantify future overexposure to EWEs, we initially identified the maximum recorded values for each metric in the historical period (1952–2016, hereafter referred to as historical threshold) for each grid cell. We then compared the predicted future values of each grid cell in each year with the historical threshold and identified the grid cells with predicted values greater than historical ones. To characterize the degree of overexposure of each grid cell for the future period (2016–2100), we calculated 2 scores: years of overexposure (i.e., number of years a given grid cell was predicted to present exposure values higher than the historical threshold) and magnitude of overexposure (i.e., difference, in the units of each metric, between the historical threshold and the maximum future value estimated for each grid cell).

We computed the overexposure scores for the metric that showed the greatest Cliff's delta for each type of EWE (Appendix S3): the number of standardized anomalies above 3 SD (nSA) for tropical cyclones, which measures intensity; the mean residency time (MRT) for heat waves, which measures duration; nSA for rainfall, which measures intensity; and the mean cumulative intensity (MCI) for droughts, which measures the interaction between intensity and duration. Details on these metrics are in Table 1.

To illustrate the usefulness of metrics for strategic conservation planning, we used the overexposure scores to delineate

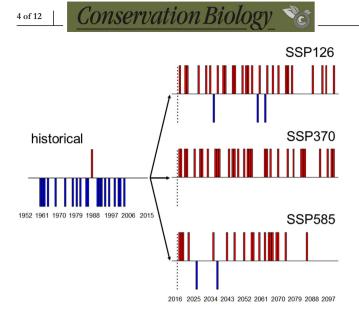


FIGURE 1 Comparison of annual exposure to extreme weather events inside and outside protected areas (PAs) from 1952 to 2100 historically and under 3 shared socioeconomic pathways (significant differences at p < 0.05; blue, exposure to EWEs is significantly greater outside PAs; red, exposure is significantly greater inside PAs; lack of a bar, no significant difference between protected and unprotected areas).

areas with conservation and/or restoration potential owing to their low exposure to future EWEs. Specifically, we identified grid cells with values below the 25th percentile of each of the 2 overexposure scores computed for each type of EWE (see above), resulting in 4 maps of the region showing cells with low exposure to intense tropical cyclones, prolonged heat waves, intense and prolonged droughts, and intense rainfall. We then overlaid the 4 maps to identify cells with low exposure to one or more extreme events.

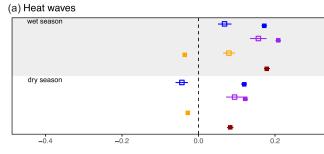
RESULTS

Our primary goal was to describe patterns of exposure under a moderate climate change scenario (SSP370). Results based on the carbon-limited (SSP126) and intensive-emissions (SSP585) scenarios are in Appendices S4 and S5. Findings with these scenarios were qualitatively similar to those of the SSP370.

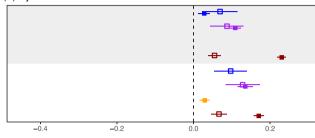
Temporal changes in exposure inside and outside PAs

Through the study period, exposure to EWEs varied between protected and unprotected areas. Before 1997, overall exposure to EWEs, as estimated by grouping all metrics, was higher outside PAs than inside. From the early 21st century onward, PAs consistently faced greater exposure to extreme events than unprotected areas, irrespective of the SSP considered (as determined by the coefficients of spatial autoregressive models with a significance level of p < 0.05) (Figure 1; Appendix S6).

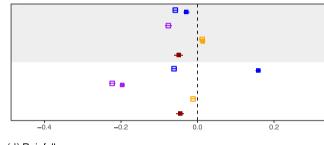
Analyzing the 32 metrics, the historically lower exposure to EWEs in PAs was estimated to increase significantly in the







(c) Droughts



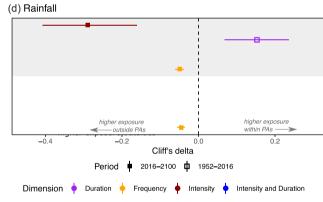


FIGURE 2 Comparison of historical and future exposure to multiple dimensions of extreme (a) heat waves, (b) cyclones, (c) drought, and (d) rainfall between protected (PA) and unprotected areas under shared socioeconomic pathway SSP370 (Cliff's delta effect size, differences in exposure; positive values, higher exposure in protected areas; negative values, higher exposure in unprotected areas; open squares, variation in exposures historically; solid squares, variation in exposures in the future; horizontal lines, 95% confidence intervals of Cliff's delta). Effect size estimates are shown for metrics that show significant differences between groups with the Wilcoxon signed-rank test (alpha <0.01). Appendix S3 contains the results of the Wilcoxon tests for all metrics and their respective effect sizes.

future (Figure 2; Appendices S3–S6). Before 2016, unprotected areas had greater exposure to heat waves of greater intensity and duration (open squares in Figure 2a) and droughts of higher intensity, frequency, and duration (open squares in Figure 2c). In contrast, PAs had higher exposure to tropical cyclone

duration (open squares in Figure 2d). As projected by the SSP370 scenario for the remainder of the 21st century, PAs and unprotected areas faced varying levels of exposure to all dimensions of change, including intensity, duration, frequency, and interactions (compare filled squares on in the positive and negative sides of the axis in Figure 2a–d). Projected impacts in PAs included exposure to more intense and prolonged heat waves (6 metrics) (Figure 2a), more intense and prolonged cyclones (6 metrics) (Figure 2) in dry and wet seasons, and more severe droughts (2 metrics) (Figure 2). Projected impacts outside PAs included exposure to more frequent heat waves (2 metrics) (Figure 2a), more severe and extended droughts (especially during the dry season) (4 metrics) (Figure 2c), and more intense and frequent rainfalls (3 metrics) (Figure 2c).

Geographical variation in projected exposure

Under the SSP370 scenario, we documented heterogeneous exposure to tropical cyclones, heat waves, droughts, and precipitation events across the Caribbean and Central America (Figure 3; Appendix S7). Despite these variations, the regions at heightened risk from each event showed consistency across different socioeconomic pathways (Appendices S8–S11).

Regarding tropical cyclones, 64.2% of the grid cells (n = 1036) in the study area were projected to experience at least one cyclone surpassing the intensity of previous extreme events. Throughout the remainder of the 21st century, a majority, about 82.1% of these cells, were projected to face high-intensity events for fewer than 21 years (orange cells in Figure 3a,b). Specifically, the Andes, Orinoco, and Amazon regions spanning Colombia, Venezuela, and Brazil were projected to experience more intense winds during the wet and dry seasons compared with the baseline period (1952–2016). In addition, the Mesoamerican corridor (stretching from South Mexico to North Colombia) will likely be exposed to considerable cyclonic activity, especially during the dry season (Figure 3a).

Heat waves presented another concern. Most grid cells, 87.5% (n = 1412), were projected to experience at least one heat wave exceeding the length of the historically longest recorded event in both seasons. Specifically, Central America was forecasted to have heat waves extending over 12 days beyond the previous record for less than one quarter of the 21st century (purple cells in Figure 3d). In contrast, the western region of South America is expected to face such extended heat waves for over half of the century's remaining duration (darkest cells in Figure 3d). Interestingly, a few areas, accounting for 19.7% of grid cells, were projected to have minimal or no overexposure. These areas were in the northeastern part of Brazil, some regions in Venezuela, and the Guianas (gray or uncolored cells in Figure 3c,d).

Approximately 61% (n = 984) and 67.6% (n = 1091) of grid cells were forecasted to experience at least one drought event surpassing the MCI of the historically most extreme dry and wet year events, respectively. Almost half of these overexposed cells might endure more severe and prolonged droughts for less

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than one quarter of the century's remaining duration (greenish cells in Appendix S7).

Conversely, precipitation levels seemed more stable. Precipitation events that exceed past records were projected to occur in 33.25% (n = 525) of grid cells. Broadly speaking, South America may experience low overexposure to heavy rainfalls. In contrast, Florida and the southeastern part of the Gulf of Mexico might face heightened overexposure, particularly during the wet season (blue cells in Appendix S7).

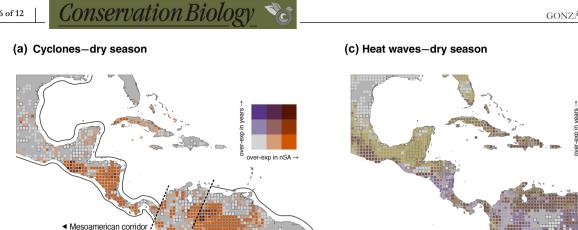
Low overexposure cells

The cells in our study area with the lowest exposure to EWEs during the 21st century are highlighted based on the convergence of 4 metrics (Figure 4). In these cells, it is anticipated that less than a quarter of the century's remaining years (<21 years) will experience EWEs of the lowest overexposure levels (<25th percentile) under the SSP370 scenario. Details for other SSPs are in Appendices S12 and S13. For the cells projected to experience the least overexposure, about 90% of them are likely to experience either one type of EWE (78.4% during the dry season and 73.8% in the wet season) or 2 types (20% in the dry and 21.8% in the wet season). Importantly, the aggregate area with low exposure varied seasonally. It decreased from 52.8% in the dry season to 39.1% in the wet season. This reduction implies an increased susceptibility to EWEs during the wet season.

DISCUSSION

PAs are the cornerstone of biodiversity conservation policy and pivotal to maintaining ecosystem functions and services (Dinerstein et al., 2020). However, the ability of PAs to achieve their conservation objectives extends beyond buffering against extractive activities and effectively managing their local biodiversity. It also depends on understanding and addressing the dynamics of global change, such as gradual warming (Peters & Darling, 1985). Despite previous studies exploring the impacts of climate change on PA viability (Araújo et al., 2011; Dobrowski et al., 2021; Hannah et al., 2007; Hoffmann & Beierkuhnlein 2020; Martinuzzi et al., 2016), our study represents the first comprehensive analysis of PAs' exposure to EWEs across Central America and the Caribbean and reveals that climate change poses substantially greater challenges in these areas compared with unprotected lands.

PAs, originally designed to preserve iconic landscapes and wildlife (Thorsell, 1990; Watson et al. 2014), may not always be adequately located to tackle the 21st-century climate crisis. Customizing strategies to effectively mitigate the impacts of EWEs is imperative to ensure the effectiveness and resilience of PAs. Our study area provides a compelling example of this imperative, where PAs in the Mesoamerican corridor and the transition from the Andes to the Orinoco and Amazon regions, previously acknowledged as refugia for gradual climate change (Griscom et al., 2020; Sales & Pires 2023), may prove insufficient without implementing measures designed to mitigate future impacts of



Transition Andes to Amazon and Orinoco basins



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(d) Heat waves-wet season

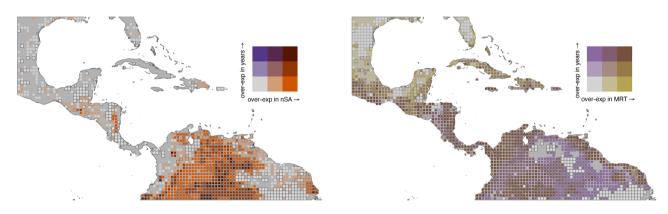


FIGURE 3 Future overexposure (over-exp) to more intense tropical cyclones in the (a) dry and (b) wet seasons and to prolonged heat waves in the (d) dry and (d) wet seasons in Central America and the Caribbean under the shared socioeconomic pathway SSP370 (colors, overexposure scores; years of overexposure, number of years in a future period in which events will be more severe than the worst event in the past; magnitude of overexposure, how extreme the worst future event will be compared with the worst past event; grid cell values, categorized as below the 25th percentile, between the 25th and 50th percentile, and above the 50th percentile; bold-bordered grid cells, over 41% of area protected; cyclone intensity, number of standardized anomalies above 3 SD [nSA]; heat wave duration, median number of consecutive days above the 95th percentile of the maximum daily temperature [mean residency time or MRT]).

tropical cyclones and heat waves in these areas (Figures 2-4). As such, our findings underscore the urgent need for management strategies that go beyond addressing gradual climate change and explicitly incorporate considerations of EWEs. Failure to do so may place species at risk. For example, a series of heat waves occurring in a compressed time frame could imperil the survival of forest species lacking suitable thermal refugia (Gonzálezdel-Pliego et al., 2020; McKechnie & Wolf 2010; Scheffers et al., 2014). Similarly, an increased likelihood of intense tropical cyclones in the near future could compromise the stability of Mesoamerican ecosystems by altering seedling establishment and recruitment (Amaral et al., 2023; Comita et al., 2009).

Adapting PAs to EWEs is more challenging than adjusting to gradual warming because biodiversity responses to EWEs depend on the specific dimension of change involved, ranging from rapid and severe disruptions to lagged long-term effects (González-Trujillo et al., 2023). For example, the more intense cyclones anticipated for the area can rapidly increase mortality rates across all developmental stages of a population, triggering mass mortality events and decreasing postdisturbance survival

rates (Frederiksen et al. 2008; Neilson et al., 2020). Conversely, events expected to become more frequent in the area, such as heat waves, are likely to have long-term effects on population dynamics by reducing recruitment and growth rates (Hughes et al., 2019; Yu et al., 2022). Finally, events that last for an extended period, such as droughts and heat waves in the area, may have delayed effects by gradually altering the recruitment process through increased mortality and reduced birth rates as the event persists (Matusick et al., 2018). As such, existing strategies for adapting to gradual climate change might not suffice for conserving biodiversity if they overlook the multifaceted threats posed by EWEs, as outlined in Table 2.

In light of our results, identification and preservation of refugia must consider future exposure to the diverse facets of EWEs. For example, areas projected to have lower overexposure to one or more types of EWEs (e.g., colored grid cells in Figure 4) could be designated as climatic refugia. These are defined as sites where biodiversity can retreat, persist, and potentially thrive amid changing environmental conditions, thereby acting as safe havens during periods of severe climatic

Recommended adaptation strategy*	Potential strengths to cope with EWEs	Potential weaknesses to cope with EWEs	Evidence
Protect climate refugia	If located in areas of low future exposure, climate refugia would protect areas and corridors that allow populations to recolonize after EWEs by serving as stepping stones and source-sink areas. If areas protect high environmental diversity, there is a high probability of capturing variability in microclimatic conditions (e.g., via microhabitats).	Refugia to gradual change may fail to shield against extreme events, as consecutive short-term extreme weather events in areas with low rates of gradual climate change can impede species from adapting to the rapidly shifting climate. Besides, a single exceptional event in a protected area may increase long-term vulnerability and reduce resilience to other types of EWEs, emphasizing the importance of comprehensive conservation planning (Ranius et al., 2023).	Historical legacies of previous heat waves and droughts amplify the lasting impacts of subsequent EWEs, leading to increased tree (Matusick et al., 2018) and coral (Fabina et al., 2015) mortality. Benthic communities are less affected by heat waves inside PAs with lower exposure zones (Sheehan et al., 2021). Protecting riparian zones as climate refugia may increase resistance to flooding and drought events (Timpane-Padgham et al., 2017).
Increase the area of current protected areas	If they are situated in areas of low current and future exposure, expanded areas would protect populations that will be a source of individuals to recolonize areas highly affected by EWEs, decreasing probability of local extinction.	Having more dispersed protected areas, instead of one large, protected area, decreases risk for EWEs, because longer distances between reserves minimize the risk that they are all affected by the same catastrophe (Shafer, 2001).	Spatial disparities in heat-wave-induced bleaching suggest that effective management targets will depend on fine-scale features, and that one-size-fits-all approaches may be less effective (Fabina et al., 2015).
Ensure sufficient connectivity	Climate corridors, if designed to not only connect warm to cold areas but also meet specific conditions, could allow for recolonization after extreme events.	Increasing landscape connectivity would not be useful for species that are unable to move to more favorable environments, especially during and after an EWE (Early & Sax 2011).	Increasing frequency and intensity of extreme storms threaten the survival of pups via impeding their dispersal (Lea et al., 2009). Connectivity with low-exposure zones around PAs enhances the resilience of benthic communities to heat waves by facilitating recolonization (Sheehan et al., 2021).
Complement permanently PAs with temporary protection	If considering the seasonal dynamics of EWEs (e.g., linked to El Niño), movable reserves may help mitigate the effect of events of different types occurring at the same location during different times of the year.	Dynamic conservation areas complement permanent PAs rather than replace them (D'aloia et al., 2019), with permanent PAs resilient to EWEs necessary for enhancing population persistence in the long term.	Temporary reserves timed with irruption events can offer a solution for protecting cultivated lands, crucial for the long-term survival of bird species during EWEs, despite their low priority in biodiversity conservation (Bateman et al., 2015). Movable reserves, if well connected to existing PAs, can aid in establishing new populations and potentially protect novel genotypes through local adaptation (Hill et al., 2011).
PAs important for biodiversity in the future	If rare species with unique ecological value are situated in zones of low future exposure, protected areas play a vital role in ensuring their long-term persistence.	Criteria such as iconic landscapes and wildlife or economic value are inadequate to protect biodiversity from the ongoing and future impacts of EWEs (Watson et al. 2014). The heightened exposure to more intense, frequent, or prolonged EWEs can render the environmental space within distributional ranges unsuitable for the future persistence of species.	Protected areas designated for their value for fisheries do not prevent heat-wave-induced impacts (Freedman et al. 2020). Under extreme climate change scenarios, assisted colonization may emerge as the sole alternative to safeguard rare and endangered species beyond their current limited distributional ranges (Liu et al., 2012).

*Recommended strategies are established following Ranius et al. (2023).

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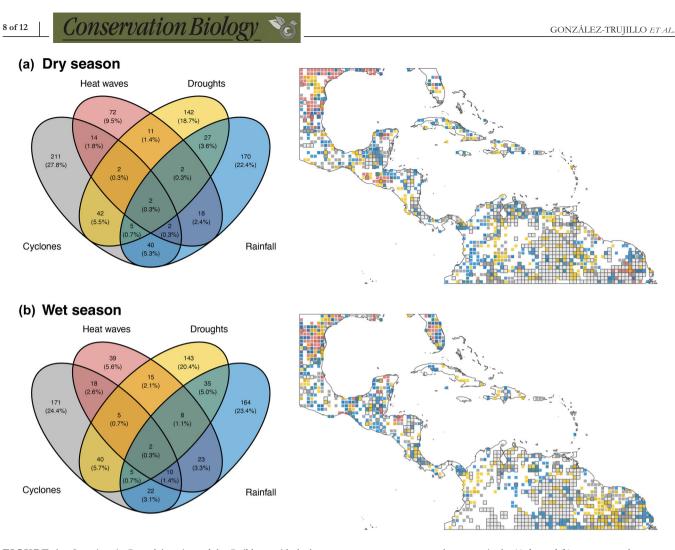


FIGURE 4 Locations in Central America and the Caribbean with the lowest exposure to extreme weather events in the (a) dry and (b) wet seasons that are anticipated to persist throughout the 21st century under the shared socioeconomic pathway SSP370 (grid cells, locations where years and magnitude of overexposure scores are below the 25th percentile; gray, tropical cyclones; red, heat waves; yellow, drought; blue, rainfall; overlapping colors, grid cell has low exposure to more than 2 event types; bold-bordered grid cells, over 41% protected area). Venn diagrams show the number of grid cells (and percentage of the total) that are predicted to have a lower level of exposure to one or more types of extreme weather events.

changes (Keppel & Wardell-Johnson 2012). Such a strategy would help safeguard species adept at weathering certain events, such as prolonged heat waves (Figure 3c), but vulnerable to others, such as intense rainfall or tropical cyclones (Figure 3a). Similarly, these areas can guide the establishment of corridors to promote source–sink dynamics and facilitate species recolonization in regions heavily affected by EWEs (Alagador et al., 2014, 2016; Williams et al., 2005). However, it is important to acknowledge the changing patterns in the seasonal exposure of EWEs (Figures 2 & 3; Appendix S7) and to view corridors as dynamic entities rather than static ones (Alagador et al., 2014, 2016; Araújo, 2009). Within this framework, corridors can serve as interim refugia, providing a buffer against short-term effects of intensifying seasonal EWE exposure, particularly in landscapes fragmented by human activity (D'aloia et al., 2019).

Although absence of knowledge on species-specific responses to EWEs might hinder effective management and conservation efforts (Bailey & van de Pol 2016; Urban et al., 2016), the use of metrics can provide valuable insights for guiding urgent and priority conservation actions (Buenafe et al.,

2023; Garcia et al., 2014; González-Trujillo et al., 2023). Our results underscore how each metric lends unique perspectives on the multiple dimensions of EWEs. By deploying a range of metrics, practitioners can discern the vulnerabilities and resilience of a specific region in terms of EWEs. This allows for a comparative analysis of regions with high and low exposure to various EWE dimensions to identify areas in need of immediate protection, restoration, or forward-looking interventions. In the context of our study region, the metrics revealed zones of overexposure that require preemptive measures, such as restoration of the Amazon and Orinoco forests to maintain thermal refugia or management of the Mesoamerican corridor to protect ecosystems from tropical cyclones during the dry season. Similarly, metrics can reveal areas with low overexposure (Figure 4) that play an important role as biodiversity corridors and offer microhabitats that buffer against extreme drought and heat wave effects (González-del-Pliego et al., 2020; Li et al., 2023; Scheffers et al., 2014). Although these metrics might not capture the full complexity of species' responses to climate change (Dawson et al., 2011; Foden et al., 2007),

their assessment often aligns with results of more sophisticated species-climate response modeling assessments (Garcia et al., 2016). As such, they can serve as a first stage broad-scope tool to identify climate-resilient areas and guide more detailed, area-specific conservation strategies in light of evolving climate change.

When making decisions on the basis of metrics, it is important to be aware of the limitations of climate data. The CMIP6 models, such as GFDL-ESM4, have improved relative to their previous renditions (Ortega et al., 2021). Nevertheless, there are still some problems with precise portravals of weather patterns in certain areas, such as South and Central America. Climate models cannot accurately predict the largest amounts of precipitation in the region, which can lead to over- or underestimation of rainfall intensity (Gouveia et al., 2022). Moreover, although frequency and spatial distribution can be recovered with good accuracy, an evident decline in performance is observed when trying to simulate the most severe cyclones and hurricanes (Roberts et al., 2020). As a result, patterns that emerge from metrics that measure the intensity of future EWEs should be interpreted with caution. A crucial step forward is to design and implement sensitivity analyses, which aid in quantifying the dependability and precision of climate change metrics derived from various climate models. This approach will facilitate informed decision-making and foster the formulation of resilient conservation and mitigation strategies, thereby safeguarding biodiversity against the challenges posed by the presently accessible data.

The Central America and Caribbean region, known for its exceptional biodiversity, has been dubbed the "miner's canary of climate change" due to the unprecedented rise in EWEs (Gould et al. 2020; Rever et al., 2017). Despite the expansion of PAs over the last century, our results showed that they are more vulnerable to EWEs than the surrounding unprotected areas. As such, climate change has put the effectiveness of PAs at a critical juncture, bringing into question the suitability of the traditional criteria used to establish them and emphasizing that new conservation strategies need to be tailored and implemented promptly. To effectively conserve regional biodiversity, conservation efforts must go beyond consideration of the effects of gradual warming and explicitly address the multidimensional impacts of EWEs. A new biodiversity conservation plan tailored to Central America and the Caribbean region should be developed, capitalizing on the opportunities presented during the 15th Conference of the Parties of the Convention for Biological Diversity. This plan should guide the identification and conservation of refugia to extreme climates, areas where species can find shelter and survive under changing conditions. Conserving refugia, where the effects of climate change are reduced, can involve expanding existing PAs or establishing temporary conservation agreements under the banner of "other effective area-based conservation measures" (IUCN WCPA Task Force on OECMs 2019). Enhancing connectivity between key biodiversity areas is also crucial to facilitating species adaptation through dispersal and therefore to enhancing the resilience of ecosystems. Additionally, adaptive management procedures, including the implementation of moveable PAs (i.e., dynamic

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regimes of land use or seasonal protection), should be considered as part of the post-2020 commitments. By adopting these comprehensive approaches, the likelihood of conserving biodiversity in the face of extreme climate change can be increased to ensure a sustainable future.

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REFERENCES

- Alagador, D., Cerdeira, J. O., & Araújo, M. B. (2014). Shifting protected areas: Scheduling spatial priorities under climate change. Journal of Applied Ecology, 51, 703-713.
- Alagador, D., Cerdeira, J. O., & Araújo, M. B. (2016). Climate change, species range shifts and dispersal corridors: An evaluation of spatial conservation models. Methods in Ecology and Evolution, 7, 853-866.
- Amaral, C., Poulter, B., Lagomasino, D., Fatoyinbo, T., Taillie, P., Lizcano, G., Canty, S., Silveira, J. A. H., Teutli-Hernández, C., Cifuentes-Jara, M., Charles, S. P., Moreno, C. S., González-Trujillo, J. D., & Roman-Cuesta, R. M. (2023). Drivers of mangrove vulnerability and resilience to tropical cyclones in the North Atlantic Basin. Science of The Total Environment, 898, Article 165413.
- Araújo, M. B. (2004). Matching species with reserves uncertainties from using data at different resolutions. Biological Conservation, 118, 533-538.
- Araújo, M. B. (2009). Protected areas and climate change in Europe. Standing Committee T-PVS/Inf (2009) 10 rev. Convention on the Conservation of European Wildlife and Natural Habitats. https://www. google.com/url?sa=t&rct=j&q=&esrc=s&source=web&cd=&ved= 2ahUKEwjLq7ay-M7_AhUYTKQEHU34D6oQFnoECAwQAQ&url= http%3A%2F%2Fwww.catedra.uevora.pt%2Frui-nabeiro%2Findex. php%2Frui_nabeiro%2Fcontent%2Fdownload%2F334%2F1903% 2Ffile%2FInf10e_2009%2520Protected%2520Areas%2520and% 2520Clim%2520Change%2520ARAUJO%2520Sept09-1.pdf&usg= AOvVaw28XOUD7T_KVzuuJZC0_Mjm&opi=89978449.
- Araújo, M. B., Alagador, D., Cabeza, M., Nogués-Bravo, D., & Thuiller, W. (2011). Climate change threatens European conservation areas: Climate change threatens conservation areas. Ecology Letters, 14, 484-492.
- Avila-Diaz, A., Torres, R. R., Zuluaga, C. F., Cerón, W. L., Oliveira, L., Benezoli, V., Rivera, I. A., Marengo, J. A., Wilson, A. B., & Medeiros, F. (2023). Current and future climate extremes over Latin America and Caribbean: Assessing Earth System models from High Resolution Model Intercomparison Project (HighResMIP). Earth Systems and Environment, 7, 99-130.
- Bailey, L. D., & Van De Pol, M. (2016). Tackling extremes: Challenges for ecological and evolutionary research on extreme climatic events. Journal of Animal Ecology, 85, 85-96.

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Conservation Biology 🗞

- Bateman, B. L., Pidgeon, A. M., Radeloff, V. C., Allstadt, A. J., Resit Akçakaya, H., Thogmartin, W. E., Vavrus, S. J., & Heglund, P. J. (2015). The importance of range edges for an irruptive species during extreme weather events. *Landscape Ecology*, 30, 1095–1110.
- Bivand, R. (2022). R packages for analyzing spatial data: A comparative case study with areal data. *Geographical Analysis*, 54, 488–518.
- Buckley, L. B., & Huey, R. B. (2016). Temperature extremes: Geographic patterns, recent changes, and implications for organismal vulnerabilities. *Global Change Biology*, 22, 3829–3842.
- Buenafe, K. C. V., Dunn, D. C., Everett, J. D., Brito-Morales, I., Schoeman, D. S., Hanson, J. O., Dabalà, A., Neubert, S., Cannicci, S., Kaschner, K., & Richardson, A. J. (2023). A metric-based framework for climate-smart conservation planning. *Ecological Applications*, 33, Article e2852.
- Castellanos, E., Castellanos, E. J., Lemos, M. F., Astigarraga, L., Chacón, N., Cuvi, N., Huggel, C., Miranda Sara, L. R., Moncassim Vale, M., Ometto, J. P., Peri, P. L., & Postigo, J. C. (2022). Central and South America. In H. O. Pörtner, D. C. Roberts, M. Tignor, E. S. Poloczanska, K. Mintenbeck, A. Alegría, M. Craig, S. Langsdorf, S. Löschke, V. Möller, A. Okem, & B. Rama (Eds.), *Climate Change 2022: Impacts, Adaptation and Vulnerability. Contribution* of Working Group II to the Sixth Assessment Report of the Intergovernmental Panel on *Climate Change* (pp. 1689–1816). Cambridge University Press.
- Chen, G., Li, X., Liu, X., Chen, Y., Liang, X., Leng, J., Xu, X., Liao, W., Qiu, Y. A., Wu, Q., & Huang, K. (2020). Global projections of future urban land expansion under shared socioeconomic pathways. *Nature Communications*, 11, Article 537.
- Cliff, N. (1993). Dominance statistics: Ordinal analyses to answer ordinal questions. *Psychological Bulletin*, 114, 494–509.
- Comita, L. S., Uriarte, M., Thompson, J., Jonckheere, I., Canham, C. D., & Zimmerman, J. K. (2009). Abiotic and biotic drivers of seedling survival in a hurricane-impacted tropical forest. *Journal of Ecology*, 97, 1346–1359.
- Cook, B. I., Smerdon, J. E., Cook, E. R., Williams, A. P., Anchukaitis, K. J., Mankin, J. S., Allen, K., Andreu-Hayles, L., Ault, T. R., Belmecheri, S., & Coats, S. (2022). Megadroughts in the Common Era and the Anthropocene. *Nature Reviews Earth & Environment*, *3*, 741–757.
- D'aloia, C. C., Naujokaitis-Lewis, I., Blackford, C., Chu, C., Curtis, J. M. R., Darling, E., Guichard, F., Leroux, S. J., Martensen, A. C., Rayfield, B., Sunday, J. M., Xuereb, A., & Fortin, M. J. (2019). Coupled networks of permanent protected areas and dynamic conservation areas for biodiversity conservation under climate change. *Frontiers in Ecology and Evolution*, 7, Article 27.
- Dawson, T. P., Jackson, S. T., House, J. I., Prentice, I. C., & Mace, G. M. (2011). Beyond predictions: Biodiversity conservation in a changing climate. *Science*, 332, 53–58.
- Dinerstein, E., Joshi, A. R., Vynne, C., Lee, A. T., Pharand-Deschênes, F., França, M., Fernando, S., Birch, T., Burkart, K., Asner, G. P., & Olson, D. (2020). A "Global Safety Net" to reverse biodiversity loss and stabilize Earth's climate. *Science Advances*, 6, Article eAbb2824.
- Dobrowski, S. Z., Littlefield, C. E., Lyons, D. S., Hollenberg, C., Carroll, C., Parks, S. A., Abatzoglou, J. T., Hegewisch, K., & Gage, J. (2021). Protected-area targets could be undermined by climate change-driven shifts in ecoregions and biomes. *Communications Earth & Environment*, 2, Article 198.
- Early, R., & Sax, D. F. (2011). Analysis of climate paths reveals potential limitations on species range shifts: Climate paths. *Ecology Letters*, 14, 1125–1133.
- Fabina, N. S., Baskett, M. L., & Gross, K. (2015). The differential effects of increasing frequency and magnitude of extreme events on coral populations. *Ecological Applications*, 25, 1534–1545.
- Foden, W., Midgley, G. F., Hughes, G., Bond, W. J., Thuiller, W., Hoffman, M. T., Kaleme, P., Underhill, L. G., Rebelo, A., & Hannah, L. (2007). A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Diversity and Distributions*, 13, 645–653.
- França, F. M., Benkwitt, C. E., Peralta, G., Robinson, J. P. W., Graham, N. A. J., Tylianakis, J. M., Berenguer, E., Lees, A. C., Ferreira, J., Louzada, J., & Barlow, J. (2020). Climatic and local stressor interactions threaten tropical forests and coral reefs. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375, Article 20190116.

- Frederiksen, M., Daunt, F., Harris, M. P., & Wanless, S. (2008). The demographic impact of extreme events: Stochastic weather drives survival and population dynamics in a long-lived seabird. *Journal of Animal Ecology*, 77, 1020–1029.
- Freedman, R. M., Brown, J. A., Caldow, C., & Caselle, J. E. (2020). Marine protected areas do not prevent marine heatwave-induced fish community structure changes in a temperate transition zone. *Scientific Reports*, 10, Article 21081.
- Garcia, R. A., Cabeza, M., Altwegg, R., & Araújo, M. B. (2016). Do projections from bioclimatic envelope models and climate change metrics match? *Global Ecology and Biogeography*, 25, 65–74.
- Garcia, R. A., Cabeza, M., Rahbek, C., & Araújo, M. B. (2014). Multiple dimensions of climate change and their implications for biodiversity. *Science*, 344, Article 1247579.
- González-del-Pliego, P., Scheffers, B. R., Freckleton, R. P., Basham, E. W., Araújo, M. B., Acosta-Galvis, A. R., Medina Uribe, C. A., Haugaasen, T., & Edwards, D. P. (2020). Thermal tolerance and the importance of microhabitats for Andean frogs in the context of land use and climate change. *Journal* of Animal Ecology, 89, 2451–2460.
- González-Trujillo, J. D., Román-Cuesta, R. M., Muñiz-Castillo, A. I., Amaral, C. H., & Araújo, M. B. (2023). Multiple dimensions of extreme weather events and their impacts on biodiversity. *Climatic Change*, 176, Article 155. https://doi.org/10.1007/s10584-023-03622-0
- Gould, W. A., Castro-Prieto, J., & Álvarez-Berríos, N. L. (2020). Climate change and biodiversity conservation in the Caribbean Islands. In M. I. Goldstein & D. A. DellaSala (Eds.), *Encyclopedia of the world's biomes* (pp. 114–125). Elsevier. https://linkinghub.elsevier.com/retrieve/pii/B9780124095489120913
- Gouveia, C. D., Rodrigues Torres, R., Marengo, J. A., & Avila-Diaz, A. (2022). Uncertainties in projections of climate extremes indices in South America via Bayesian inference. *International Journal of Climatology*, 42, 7362– 7382.
- Gräler, B., Pebesma, E., & Heuvelink, G. (2016). Spatio-temporal interpolation using gstat. *The R Journal*, 8, 204–218.
- Griscom, B. W., Busch, J., Cook-Patton, S. C., Ellis, P. W., Funk, J., Leavitt, S. M., Lomax, G., Turner, W. R., Chapman, M., Engelmann, J., Gurwick, N. P., Landis, E., Lawrence, D., Malhi, Y., Schindler Murray, L., Navarrete, D., Roe, S., Scull, S., Smith, P., ... Worthington, T. (2020). National mitigation potential from natural climate solutions in the tropics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375, Article 20190126.
- 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, 131–138.
- Harris, R. M. B., Beaumont, L. J., Vance, T. R., Tozer, C. R., Remenyi, T. A., Perkins-Kirkpatrick, S. E., Mitchell, P. J., Nicotra, A. B., Mcgregor, S., Andrew, N. R., Letnic, M., Kearney, M. R., Wernberg, T., Hutley, L. B., Chambers, L. E., Fletcher, M.-S., Keatley, M. R., Woodward, C. A., Williamson, G., ... Bowman, D. M. J. S. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change*, *8*, 579–587.
- Hill, J. K., Griffiths, H. M., & Thomas, C. D. (2011). Climate change and evolutionary adaptations at species' range margins. *Annual Review of Entomology*, 56, 143–159.
- Hoffmann, S., & Beierkuhnlein, C. (2020). Climate change exposure and vulnerability of the global protected area estate from an international perspective. *Diversity and Distributions*, 26, 1496–1509.
- Hughes, T. P., Kerry, J. T., Connolly, S. R., Baird, A. H., Eakin, C. M., Heron, S. F., Hoey, A. S., Hoogenboom, M. O., Jacobson, M., Liu, G., Pratchett, M. S., Skirving, W., & Torda, G. (2019). Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nature Climate Change*, 9, 40–43.
- Intergovernmental Panel on Climate Change (IPCC). (2021). Framing, context, and methods. In V., Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change* (pp. 147–286). Cambridge University Press. https://www.cambridge.org/core/product/ identifier/9781009157896/type/book

Conservation Biology 🔏

- IUCN WCPA Task Force on OECMs. (2019). Recognising and reporting other effective area-based conservation measures. International Union for Conservation of Nature. https://portals.iucn.org/library/node/48773
- Keppel, G., & Wardell-Johnson, G. W. (2012). Refugia: Keys to climate change management. *Global Change Biology*, 18, 2389–2391.
- Kreyling, J., Jentsch, A., & Beier, C. (2014). Beyond realism in climate change experiments: Gradient approaches identify thresholds and tipping points. *Ecology Letters*, 17, 125-e1.
- Lange, S., Volkholz, J., Geiger, T., Zhao, F., Vega, I., Veldkamp, T., Reyer, C. P., Warszawski, L., Huber, V., Jägermeyr, J., & Schewe, J. (2020). Projecting exposure to extreme climate impact events across six event categories and three spatial scales. *Earth's Future*, 8, Article e2020EF001616. https:// onlinelibrary.wiley.com/doi/10.1029/2020EF001616
- Lea, M.-A., Johnson, D., Ream, R., Sterling, J., Melin, S., & Gelatt, T. (2009). Extreme weather events influence dispersal of naive northern fur seals. *Biology Letters*, 5, 252–257.
- Li, D., Memmott, J., & Clements, C. F. (2023). Corridor quality buffers extinction under extreme droughts in experimental metapopulations. *Ecology and Evolution*, 13, Article e10166.
- Liu, H., Feng, C.-L., Chen, B.-S., Wang, Z.-S., Xie, X.-Q., Deng, Z.-H., Wei, X.-L., Liu, S.-Y., Zhang, Z.-B., & Luo, Y.-B. (2012). Overcoming extreme weather challenges: Successful but variable assisted colonization of wild orchids in southwestern China. *Biological Conservation*, 150, 68–75.
- Martinuzzi, S., Allstadt, A. J., Bateman, B. L., Heglund, P. J., Pidgeon, A. M., Thogmartin, W. E., Vavrus, S. J., & Radeloff, V. C. (2016). Future frequencies of extreme weather events in the National Wildlife Refuges of the conterminous U.S. *Biological Conservation*, 201, 327–335.
- Matusick, G., Ruthrof, K. X., Kala, J., Brouwers, N. C., Breshears, D. D., & Hardy, G. E. S. H. (2018). Chronic historical drought legacy exacerbates tree mortality and crown dieback during acute heatwave-compounded drought. *Environmental Research Letters*, 13, Article 095002.
- Mckechnie, A. E., & Wolf, B. O. (2010). Climate change increases the likelihood of catastrophic avian mortality events during extreme heat waves. *Biology Letters*, 6, 253–256.
- Neilson, E. W., Lamb, C. T., Konkolics, S. M., Peers, M. J. L., Majchrzak, Y. N., Doran-Myers, D., Garland, L., Martinig, A. R., & Boutin, S. (2020). There's a storm a-coming: Ecological resilience and resistance to extreme weather events. *Ecology and Evolution*, 10, 12147–12156.
- Ortega, G., Arias, P. A., Villegas, J. C., Marquet, P. A., & Nobre, P. (2021). Present-day and future climate over central and South America according to CMIP5 /CMIP6 models. *International Journal of Climatology*, 41, 6713–6735.
- Pecl, G. T., Araújo, M. B., Bell, J. D., Blanchard, J., Bonebrake, T. C., Chen, I.-C., Clark, T. D., Colwell, R. K., Danielsen, F., Evengård, B., Falconi, L., Ferrier, S., Frusher, S., Garcia, R. A., Griffis, R. B., Hobday, A. J., Janion-Scheepers, C., Jarzyna, M. A., Jennings, S., ... Williams, S. E. (2017). Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science*, 355, Article eaai9214.
- Pereira, H. M., Navarro, L. M., & Martins, I. S. (2012). Global biodiversity change: The bad, the good, and the unknown. *Annual Review of Environment* and Resources, 37, 25–50.
- Perkins, S. E., & Alexander, L. V. (2013). On the measurement of heat waves. *Journal of Climate*, 26, 4500–4517.
- Peters, R. L. (1985). The greenhouse effect and nature reserves. *BioScience*, 35, 707–717.
- Ranius, T., Widenfalk, L. A., Seedre, M., Lindman, L., Felton, A., Hämäläinen, A., Filyushkina, A., & Öckinger, E. (2023). Protected area designation and management in a world of climate change: A review of recommendations. *Ambio*, 52, 68–80.
- R Core Team. (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project. org/
- Reyer, C. P. O., Adams, S., Albrecht, T., Baarsch, F., Boit, A., Canales Trujillo, N., Cartsburg, M., Coumou, D., Eden, A., Fernandes, E., Langerwisch,

F., Marcus, R., Mengel, M., Mira-Salama, D., Perette, M., Pereznieto, P., Rammig, A., Reinhardt, J., Robinson, A., ... Thonicke, K. (2017). Climate change impacts in Latin America and the Caribbean and their implications for development. *Regional Environmental Change*, *17*, 1601–1621.

- Roberts, M. J., Camp, J., Seddon, J., Vidale, P. L., Hodges, K., Vannière, B., Mecking, J., Haarsma, R., Bellucci, A., Scoccimarro, E., Caron, L.-P., Chauvin, F., Terray, L., Valcke, S., Moine, M. P., Putrasahan, D., Roberts, C. D., Senan, R., Zarzycki, C., ... Wu, L. (2020). Projected future changes in tropical cyclones using the CMIP6 HighResMIP multimodel ensemble. *Geophysical Research Letters*, 47, Article e2020GL088662.
- Sabater, S., Freixa, A., Jiménez, L., López-Doval, J., Pace, G., Pascoal, C., Perujo, N., Craven, D., & González-Trujillo, J. D. (2022). Extreme weather events threaten biodiversity and functions of river ecosystems: Evidence from a meta-analysis. *Biological Reviews*, 98(2), 450–461.
- Sales, L. P., & Pires, M. M. (2023). Identifying climate change refugia for South American biodiversity. *Conservation Biology*, 37, Article e14087.
- Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., & Evans, T. A. (2014). Microhabitats reduce animal's exposure to climate extremes. *Global Change Biology*, 20, 495–503.
- Shafer, C. L. (2001). Inter-reserve distance. Biological Conservation, 100, 215-227.
- Sheehan, E. V., Holmes, L. A., Davies, B. F. R., Cartwright, A., Rees, A., & Attrill, M. J. (2021). Rewilding of protected areas enhances resilience of marine ecosystems to extreme climatic events. *Frontiers in Marine Science*, 8, Article 671427.
- Sillmann, J., Kharin, V. V., Zhang, X., Zwiers, F. W., & Bronaugh, D. (2013). Climate extremes indices in the CMIP5 multimodel ensemble: Part 1. Model evaluation in the present climate. *Journal of Geophysical Research: Atmospheres*, 118, 1716–1733.
- Smale, D. A., & Wernberg, T. (2013). Extreme climatic event drives range contraction of a habitat-forming species. *Proceedings of the Royal Society B: Biological Sciences*, 280, Article 20122829.
- Taylor, M. A., Stephenson, T. S., Chen, A. A., & Stephenson, K. A. (2012). Climate change and the Caribbean: Review and response. *Caribbean Studies*, 40, 169–200.
- Thompson, V., Mitchell, D., Hegerl, G. C., Collins, M., Leach, N. J., & Slingo, J. M. (2023). The most at-risk regions in the world for high-impact heatwaves. *Nature Communications*, 14, Article 2152.
- Thorsell, J. W. (1990). Research in tropical protected areas: Some guidelines for managers. *Environmental Conservation*, 17, 14–18.
- Timpane-Padgham, B. L., Beechie, T., & Klinger, T. (2017). A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. *PLoS ONE*, 12, Article e0173812.
- Torchiano, M. (2020). effsize: Efficient effect size computation. https://CRAN.Rproject.org/package=effsize
- Urban, M. C., Bocedi, G., Hendry, A. P., Mihoub, J.-B., Pe'er, G., Singer, A., Bridle, J. R., Crozier, L. G., De Meester, L., Godsoe, W., Gonzalez, A., Hellmann, J. J., Holt, R. D., Huth, A., Johst, K., Krug, C. B., Leadley, P. W., Palmer, S. C. F., Pantel, J. H., ... Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, 353, Article aAd8466.
- Ver Hoef, J. M., Peterson, E. E., Hooten, M. B., Hanks, E. M., & Fortin, M. J. (2018). Spatial autoregressive models for statistical inference from ecological data. *Ecological Monographs*, 88, 36–59.
- Watson, J. E. M., Dudley, N., Segan, D. B., & Hockings, M. (2014). The performance and potential of protected areas. *Nature*, 515, 67– 73.
- Wethey, D. S., Woodin, S. A., Hilbish, T. J., Jones, S. J., Lima, F. P., & Brannock, P. M. (2011). Response of intertidal populations to climate: Effects of extreme events versus long term change. *Journal of Experimental Marine Biology and Ecology*, 400, 132–144.
- Williams, P., Hannah, L., Andelman, S., Midgley, G., Araújo, M., Hughes, G., Manne, L., Martinez-Meyer, E., & Pearson, R. (2005). Planning for climate change: Identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology*, 19, 1063–1074.

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Conservation Biology 🗞

Yu, X. L., Li, J.-Y., Zhou, Y.-T., Peng, J., & Qiu, B.-L. (2022). Simulated extreme high temperatures alter the demographic parameters of *Aphelinus asychis* and diminish parasitoid fitness. *Biological Control*, 174, Article 105028.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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