Planning for current species distributions is more effective than planning for nature's stage in the face of climate change

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Abstract

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Climate change poses a significant threat to biodiversity. Increasing the number and size of protected areas is one of the most frequently cited approaches to addressing this threat. However, because climate change is already shifting species distributions, traditional reserve-selection strategies that rely on current patterns of biodiversity may be ineffective. One commonly suggested alternative is to protect geophysical diversity, or the various edaphic, topographic, elevational, and geographical features of a landscape. As climate change continues to drive changes in species distributions, geophysically diverse landscapes may have the potential to provide the habitat heterogeneity needed to accommodate new ranges of species. We use projected climate-driven shifts in species distributions to compare the effectiveness of reserve networks designed to increase the representation of today's species distributions to the effectiveness of reserve networks built to increase the protection of geophysical diversity. Reserve networks built with biological targets protected up to 18% more species than reserve networks built with geophysical targets and geophysical networks protected few more species than did randomly selected networks. These patterns were consistent across future climate scenarios with varying levels of change. Our results indicate that prioritizing areas for protection based on current patterns of biodiversity is likely to be more effective at protecting future patterns of biodiversity than prioritizing areas based on geophysical diversity.

Introduction

Climate change is affecting the natural world and, in turn, how managers plan for resilient ecosystems. In the next century, climate change is expected to cause extinctions, range shifts and contractions, and increase the spread of invasive species (IPCC, 2014). As species distributions shift due to climate change, many species are likely to move into or out of existing reserves and reserve networks (Araújo et al., 2004). Hence, the current reserve system may not adequately account for the long-term persistence of biodiversity (Heller and Zavaleta, 2009). Expanding the availability and connectivity of protected habitat, or reserves, has been cited as a potentially effective method for protecting biodiversity in a changing climate (Groves et al., 2012). Reserve networks designed to allow for movement both within and among reserves have the potential to increase species' capacities to adjust to changes in the climate (Carroll et al., 2015).

Given the potential impacts of climate change on species distributions, several alternatives to the traditional species-based approach to reserve network design have been suggested, including: protecting remaining large, intact landscapes and ecological processes, maintaining and improving ecological connectivity, and protecting climate refugia (Schmitz et al., 2015). Despite the variety of proposed responses, one approach has received more attention and support than have others. The approach involves protecting areas that harbor a diversity of abiotic conditions (hereafter geophysical settings or geophysical diversity, but also referred to as land facets) and the approach has been referred to as "conserving nature's stage" (Beier et al., 2015). Geophysical diversity refers to the variety of edaphic, topographic, and geographical conditions of a landscape. These geophysical features influence the local climate and the availability of resources, such as water, which thereby determine, in part, species composition

(Lawler et al., 2015). Geophysical settings are unique combinations of geophysical features that can be described across a region. For example, in The Nature Conservancy's 2015 report on Pacific Northwest resilient landscapes, authors defined 162 geophysical settings by categorizing soil order, elevation, and slope, and cross-tabulating these groups (Buttrick et al., 2015). The topographic position—defined by slope, aspect, and elevation—of a landscape feature indirectly influences local biodiversity by driving near-surface air temperature and water availability due to varying wind patterns and solar exposure (Dobrowski, 2011). In complex, mountainous terrain, pockets of significant topographic shading and wind protection can result in cold-air pooling (Lundquist and Cayan, 2007). These cold-air pools provide cool, moist habitats to which snow-dwelling animals such as the wolverine (*Gulo gulo*) can retreat during periods of adverse environmental conditions (see Curtis et al., 2014; Gavin et al., 2014). Aspect also significantly influences soil structure by controlling the amount of precipitation and snowmelt infiltrating into watershed soils, thereby influencing habitat diversity (Geroy et al., 2011). Edaphic heterogeneity has been shown to be an important driver of speciation and biodiversity (e.g. Fine et al., 2005).

The geophysical settings approach stems from the hypothesis that species richness is positively correlated with habitat heterogeneity. In 1890, Merriam proposed the Life Zone Concept, which asserts that plant and animal communities are associated with specific environments. Yet species ranges are not stationary through space and time—they move and adapt to environmental and climatic changes. In the face of anthropogenic climate change, prioritizing landscapes with relatively higher geophysical diversity is gaining traction as a strategy for reserve network design because it is expected to facilitate dispersal, support high species richness, and protect individual species of concern (Lawler et al., 2015; Anderson and Ferree, 2010). Furthermore, some scientists argue that even if species composition shifts with changing environmental conditions, preservation of geophysical diversity will continue to support biologically diverse communities by protecting the heterogeneous environment needed for evolutionary and ecological adaptation (Beier and Brost, 2010).

Several researchers have promoted the use of geophysical diversity in the conservation planning process as a strategy for addressing climate change, and much has been invested in it. There is ample evidence for the influence of environmental factors on species' ranges, though the relationship is not without some uncertainties. To date, no tests of this strategy have been conducted. Here, we perform such a test using projected climate-driven changes in species distributions in the western United States. We developed reserve networks based on current patterns of biodiversity and reserve networks based on geophysical settings, using both complementarity and richness-based site prioritization. We then used projected future distributions of 547 plant and animal species to evaluate the effectiveness of both approaches.

Methods

Study Area

The study covered ten states in the western United States: Washington, Oregon, California, Idaho, Nevada, Montana, Wyoming, Utah, Colorado, and Arizona—in total roughly 2.7M km^2 ranging from approximately 31° 20' N to 49° N latitude, and 102° 03' W to 124° 26' W longitude. Elevation in the study area extends from sea level to 4421-m and the area spans a diversity of climatic and edaphic conditions including deserts, alpine zones, and temperate forests. We defined geophysical settings and projected species distributions at a 1-km^2 resolution to maximize both geophysical and biological relevance, while minimizing computational requirements.

Defining Geophysical Settings

We defined geophysical settings according to Michalak et al. (2015) by cross-tabulating four edaphic and topographic spatial datasets: elevation, landforms, modified heat load index, and soil order. Elevation data were derived from SRTM v4.1 below 60 degrees N and from ASTER GDEM v2 above 60 degrees N (NASA, 2009). We binned elevations into two classes for each of five vegetation life zones (plains, foothills, montane, subalpine, and alpine), resulting in 10 elevation classes. Landforms were classified based on a topographic position index and slope, producing both broad-scale landforms such as mountains and canyons and finer scale features such as headwaters and hilltops. Heat load indices incorporate slope and aspect to estimate solar insolation. We modified the heat load index developed by McCune and Leon (2002) to remove the effect of latitude and define more relevant physical habitat types. We divided the index values into three categories: cool, neutral, and warm. Soil order (n=38) is associated with soil moisture, temperature, and physical and chemical properties. Cross-tabulating these classifications produced 1,068 unique combinations of the geophysical features at a 1-km^2 resolution.

Biodiversity Conservation Elements

We developed species distribution models (SDMs) for 238 animal species and 309 plant species. The 547 species included in our study were selected based on their location, availability of occurrence data, and status listed by the International Union for Conservation of Nature (IUCN). Presence-only occurrence data for all 547 species were obtained from the Global Biodiversity Information Facility (GBIF; http://www.gbif.org/occurrence). Species with fewer than 25 recorded occurrences were excluded from this analysis. All species currently known to inhabit the study area and categorized by the IUCN as Least Concern, Near Threatened, Vulnerable, Endangered, or Critically Endangered were included.

We built all SDMs using Maxent software. Maxent models species distributions using a machine-learning approach based on the principle of maximum entropy. The software uses a set of environmental (in this case, climatic) grids and spatially-explicit occurrence data to predict habitat suitability for each species across the defined study area. In comparison to other SDM software, Maxent performs particularly well with presence-only data (Phillips et al., 2009). Maxent defines pseudo-absences by randomly sampling the landscape (Merow et al., 2013). Pseudo-absences were generated for each species in an area proportionally larger than the extent of its current distribution. The probability of presence for a given species at a location is estimated from training and testing data consisting of both presences and pseudo-absences. In addition to probability rasters, we generated binary presence-absence rasters using the optimal threshold, which was calculated by maximizing the sum of the sensitivity and the specificity of the training dataset, minimizing both false-positive and false-negative errors. We accounted for potential spatial bias in sampling efforts and occurrence data by using bias layers that described the distribution of occurrences for each taxon (Elith et al., 2011).

We projected potential ranges for each of the 547 species both in the current climate and under 12 future climatic scenarios, producing a total of 7,111 raster maps. We forecast each species' potential future distribution based on the projections of three General Circulation Models (GCMs), two greenhouse gas emissions scenarios, and two time periods. INMCM4, MIROC5, and GFDL-CM3 were selected to be GCMs representative of mild, moderate, and considerable change, respectively (Fick and Hijmans, 2017). For emissions scenarios, we used the representative concentration pathways (RCP) 4.5 and 8.5. Emissions in the RCP 4.5 scenario peak around 2040 and decline thereafter, and emission in the RCP 8.5 scenario continue to rise throughout the 21st century (Meinshausen et al., 2011).We projected future species distributions into the 2050's (averaged projections from 2041 to 2060) and the 2070's (averaged projections from 2061 to 2080). We chose the 2050's to provide a realistic window for planning and management. The results from projections made for the 2070's were used to evaluate whether our conclusions would change over time as species continue to move. We used 19 bioclimatic variables derived from monthly temperature and precipitation values.

Sites

We defined sites for reserve selection using sixth-level (sub-watershed) hydrologic unit codes (HUC-12, $n_{huc-12} = 28{,}503$; hereafter sites). The average size of these sites was 95.1 km^2 ($s = 61.43$). We tallied the number of 1-km^2 cells occupied by each species and the number of cells of each type of geophysical setting in each site. We chose these sub-watersheds for sites because they are both ecologically relevant and of a reasonably applicable size for conservation planning purposes. For example, most ecoregional assessments by The Nature Conservancy use sixth-level sub-watersheds as planning units (Buttrick et al., 2015).

Prioritizing Areas for Conservation

We prioritized sites to be included in theoretical reserve networks designed to capture either today's biodiversity or geophysical diversity. We compared the two reserve networks by quantifying the effectiveness of each at protecting species in the twelve future climatic scenarios. We selected reserve networks using Marxan (Ball et al., 2009).

Marxan was originally developed to solve a version of the minimum set reserve design problem by minimizing costs and boundary lengths of the whole system, while simultaneously meeting biodiversity targets. Marxan uses simulated annealing, a stochastic optimization process, to iteratively find reserve networks that maximize costs. One generally runs the algorithm multiple times producing replicate reserve networks. The output is essentially lists of sites that together form networks. One can assign an importance to each site based on its estimated "irreplaceability." The more frequently each site is selected, the greater its irreplaceability value. A site is completely irreplaceable if it is selected in all iterations.

We prioritized sites to complement the protection afforded by the existing protected area network, which covers nearly 13% of the study area. We identified protected lands using the Protected Areas Database of the U.S. (PADUS), and only included land with gap codes "1" and "2" (USGS). Land designated as gap codes 1-2 have the highest degree of protection, and do not include areas that allow multiple uses such as resource extraction. We labeled a site as protected if at least 50% of its area was designated under gap codes 1 or 2 by PADUS. Each site that was designated as an existing protected area was fixed in the initial reserve network and could not be removed (Game and Grantham, 2008). At the 50% threshold, 3,118 sites were considered existing protected areas, which amounts to approximately 11% of the study area (Fig. 1). Because the choice of the 50% threshold had the potential to affect our results, we also built networks using an 80% threshold and compared our main results to those derived from these additional networks. Finally, we built unconstrained networks, or networks built without considering any site an existing protected area. In comparison to constrained results, the unconstrained analysis demonstrates the influence of the existing protected area system on the performance of each approach to reserve network design.

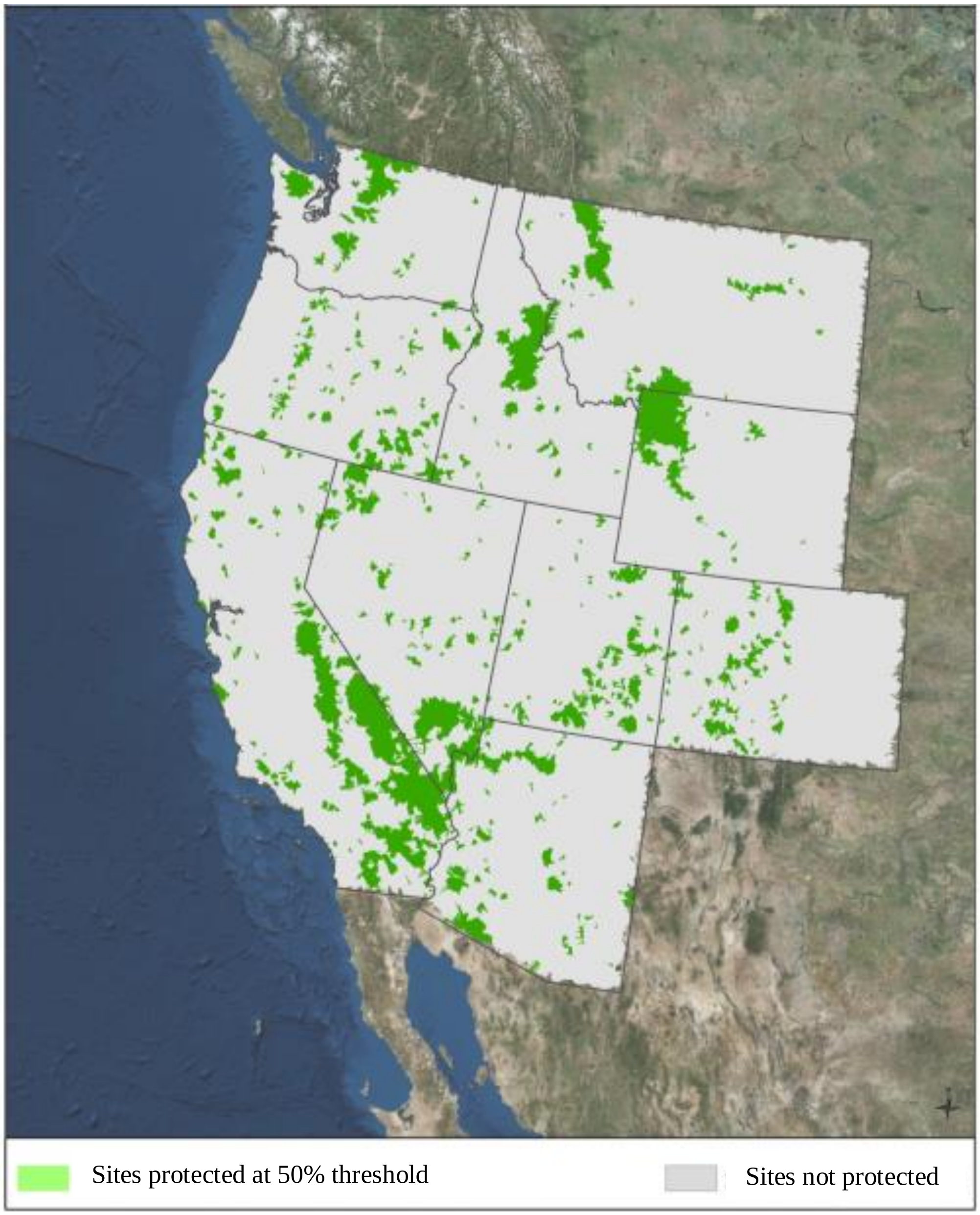


Figure 1. Sites considered protected at a 50% threshold. *These sites (n= 3,118) were considered existing protected areas, and thereby required to be included in each simulated reserve network iteration.*

We required reserve networks to cover at least 20% of the current distribution of each species or geophysical setting. According to Tear et al., 2005, many initial global biodiversity protection goals that were set at 10%, while politically achievable, were ecologically insufficient and a more effective goal would be closer to 30% of each planning region. Therefore, to account for both politically and ecologically relevant goals, we also tested the effectiveness of reserve networks at protecting 10% and 30% of each target's distribution.

We selected multiple networks of different sizes for biological and geophysical targets. By building a series of networks of increasing size, we were able to compare an accumulation curve for species to an accumulation curve for geophysical settings. The smallest reserve networks included only the 50 targets with the smallest distributions, and increased in size as we added more widely distributed targets in increments of 50. This resulted in 11 biological Marxan runs and 22 geophysical Marxan runs per analytical variation. Each network was the result of 100 Marxan runs that each involved 100M iterations. To evaluate the effectiveness of the reserve networks at representing the projected future ranges of species, we used the "best" network from the 100 replicate Marxan runs. Marxan ranks and evaluates networks based on the number of targets (species or geophysical settings) represented by the reserve network and the total cost of the sites in the network. The "best" network would thus be the cheapest one that represented all targets. We also explored the effectiveness of the top 10 Marxan solutions and averaged the results of those evaluations. Because we found no qualitative differences in the averaged and the best results, we report only the results of the best Marxan solutions here. In the absence of land costs for each site, we used site area as a crude proxy for cost.

We evaluated how well each of the nine reserve network variations performed in each of the 12 future climate scenarios. We quantified the level of effectiveness by spatially intersecting the SDMs in each climate scenario with a given reserve network and summing the number of species that it protects. A species was considered protected if the amount of its future distribution covered by the reserve was greater than 20% of its current distribution. For example, the American pika's (*Ochotona princeps*) current distribution covers approximately 150,000-km^2 in the study area. A reserve network would have cover a minimum of 30,000-km^2 of the pika's future distribution for the species to be considered protected. The species' current distribution provided a baseline indicator of future distribution requirements. We used the 20% species protection threshold to be consistent with the parameter that we used in our reserve network design analysis. For the reserve networks in our secondary analysis, those designed to protect 10% or 30% of each species current distribution, we used a 10% and 30% species protection threshold, respectively.

Additionally, we compared the relative effectiveness of the two methods of reserve network designs when they were designed solely for plants and solely for animals. For this analysis, we created reserve networks in Marxan based on either plant or animal species targets, and compared them to the reserve networks based on geophysical settings.

We also compared the effectiveness of the species-based and geophysical settings based reserve networks to randomly selected networks. We created 15 random networks ranging in size from 3,500 to 7,100 sites by adding randomly selected sites to the existing reserve network. For each size of random network, we generated 20 replicate networks, evaluated the effectiveness of each network at representing projected future species distributions, and averaged the 20 resulting values.

Irreplaceability

We compared the irreplaceability of sites for representing today's species distributions to the irreplaceability of sites for representing geophysical settings. We calculated irreplaceability as the number of times that a site was included in the 100 networks generated by the 100 Marxan runs.

Richness Analysis

The analyses mentioned thus far are based on the concept of complementarity. Complementarity in reserve network design is the degree to which a site adds unrepresented targets to the existing network of sites (Margules and Pressey, 2000). However, conservation biologists and practitioners have also recommended prioritizing sites with the highest richness in geophysical settings as areas to protect. To test this reserve network design method, we created reserve networks based on site richness in geophysical settings and species, respectively. To create the reserve networks in this analysis, we selected the sites with the highest richness value per larger watershed. For the larger watersheds, we used four-digit hydrologic unit code subregions (HUC-4, $n_{huc-4} = 66$). We quantified richness by simply summing the number of species per site and the number of geophysical settings per site. We compared reserve networks designed with species to reserve networks designed with geophysical settings. To design a comparable analysis to the complementarity analysis, we developed richness reserve networks across a range of sizes. We created randomly selected reserve networks for the richness analysis by adding a percentage of randomly selected sites per sub-region to the existing reserve network. Again, we averaged the results of 20 random repetitions. We evaluated the reserve networks based on richness using the same methods we used to evaluate those based on complementarity.

Results

Reserve networks created with current patterns of biodiversity were more effective at protecting future patterns of biodiversity than were reserve networks designed based on geophysical diversity (Fig. 2). Geophysical reserve networks performed only marginally better than the randomly generated networks. These patterns were consistent across all 12 climate-change scenarios (Fig. S1). For example, protecting approximately 16% (424,000 km^2) of the landscape using today's biodiversity as the target resulted in between 18.3% and 18.8% more species being protected in the 2050s and between 13.4% and 18.3% more species being protected in the 2070s than did using the geophysical settings as targets. Protecting the same amount of the landscape using geophysical settings protected at most 5.6% more species than did sites selected at random.

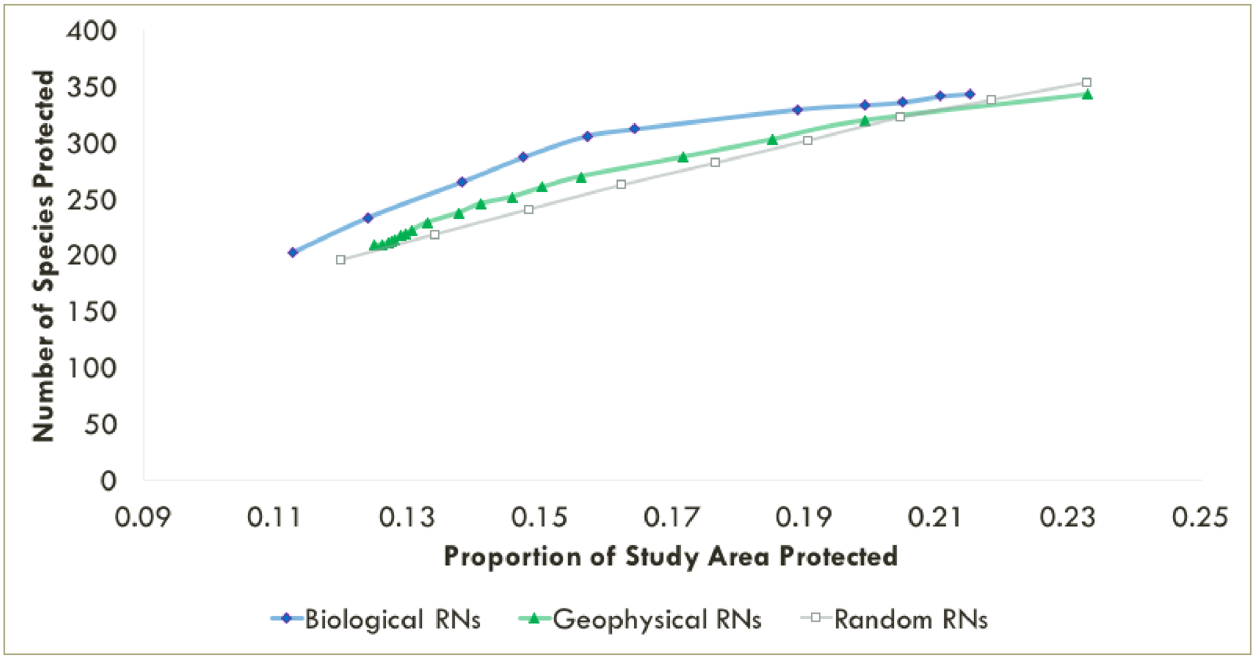


Figure 2. Results from the extreme emissions scenario (8.5) and 2070 time-period, averaged across mild, moderate, and considerable GCMs.

The degree to which current biodiversity outperformed geophysical settings depended on the amount of land included the reserve networks, the level of projected climatic change, and the taxonomic group being considered. For example, the disparity between biological and geophysical reserve networks decreases as the climate projections become more extreme, either in emission scenario, time-period, or GCM. To parse out the driver behind this disparity, we averaged our results across the two emissions scenarios, two time-periods, and three GCMs for a particular reserve network size (Fig. 3). To demonstrate the most extreme example of this disparity, we selected the reserve network size at which there is the greatest difference between the two types, that is at roughly 16% of the study area. Again, we found that biological reserve networks consistently perform more effectively than geophysical reserve networks across climate scenario variables. However, as the climate scenario becomes more extreme, biological reserve networks tend to decrease in effectiveness whereas the effectiveness of geophysical reserve networks tends to remain stable or marginally increase.

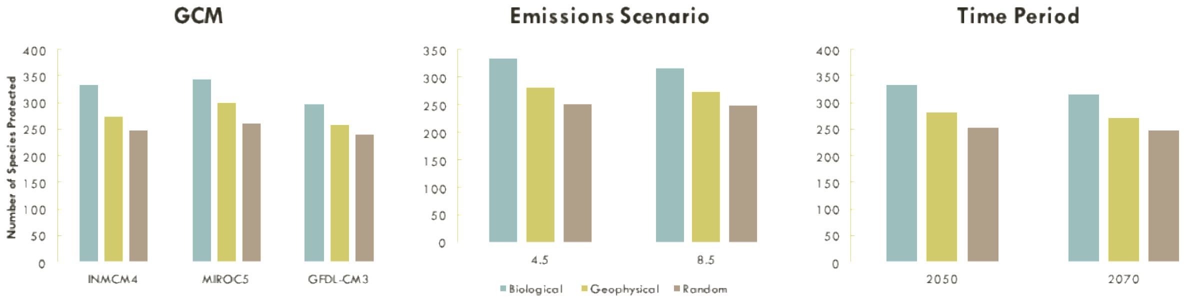


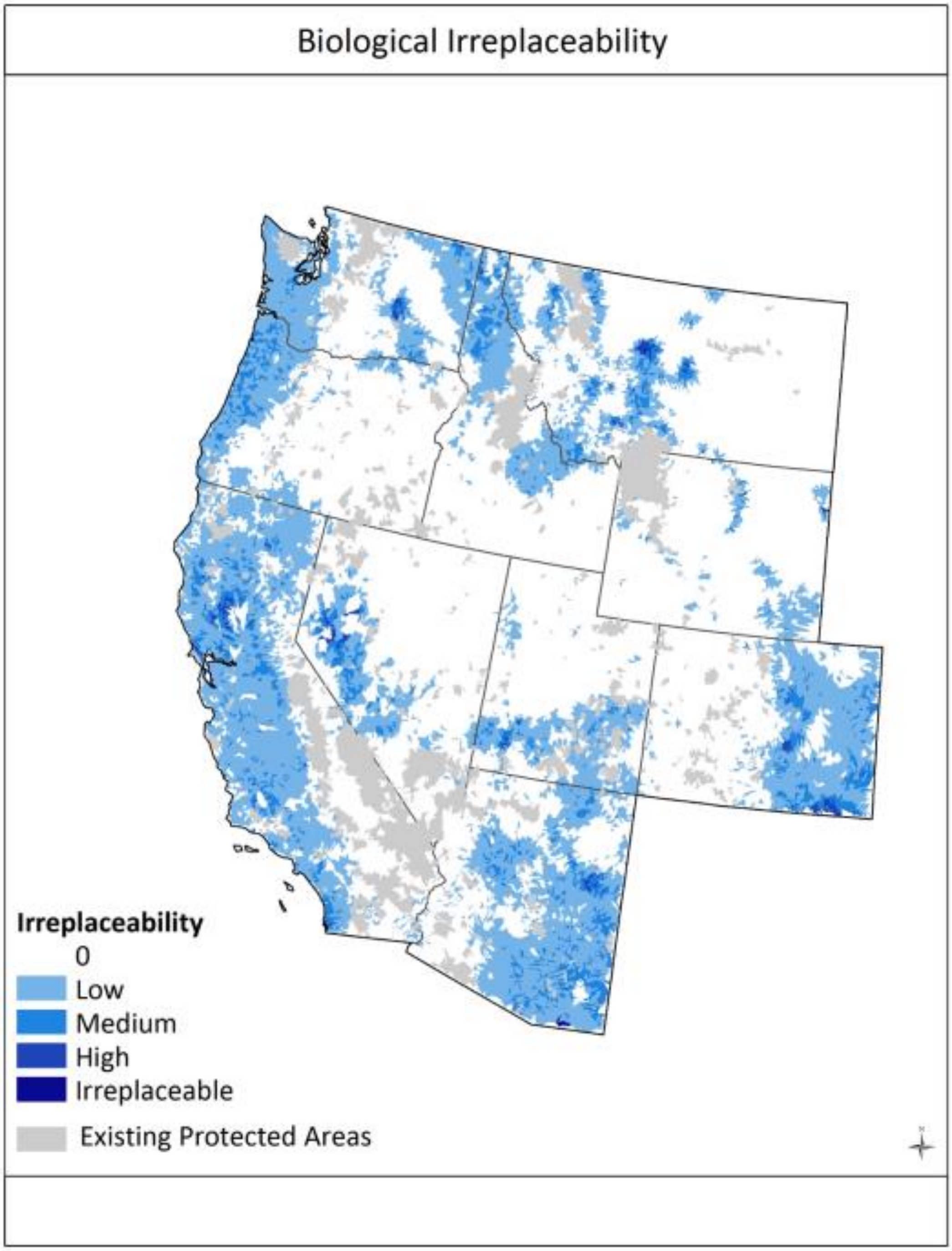
Figure 3. Averaged results for each climate scenario variable: time-period, GCM, and emissions scenario. The reserve networks in this chart cover roughly 16% of the study area.

In our taxonomic grouping analysis, we found that the effectiveness of geophysical reserve networks differed among plant and animals. Geophysical reserve networks, on average, protect 5.35% more plants than they did animals. However, reserve networks built with only plants or only animals as targets are still more effective than reserve networks built with geophysical diversity at protecting the respective taxonomic groups.

The networks of sites selected to protect current species distributions and the networks selected to protect geophysical settings also differed markedly in their spatial arrangement (Fig.

4A-B). Sites in geophysical reserve networks were far more scattered throughout the western U.S. than were sites selected to protect current species distributions. In addition, sites selected to protect geophysical settings were generally less irreplaceable (more interchangeable) than were sites selected to protect current biodiversity. Sites with more unique or rare entities (species or geophysical settings) tend to be more irreplaceable, whereas sites with common elements tend to be more interchangeable. We also found relatively few sites deemed to be important (highly irreplaceable) for both protecting current species distributions and protecting geophysical settings (Fig. 5).

A.


Biological Irreplaceability
Irreplaceability
0
Low
Medium
High
Irreplaceable
Existing Protected Areas
N

B.

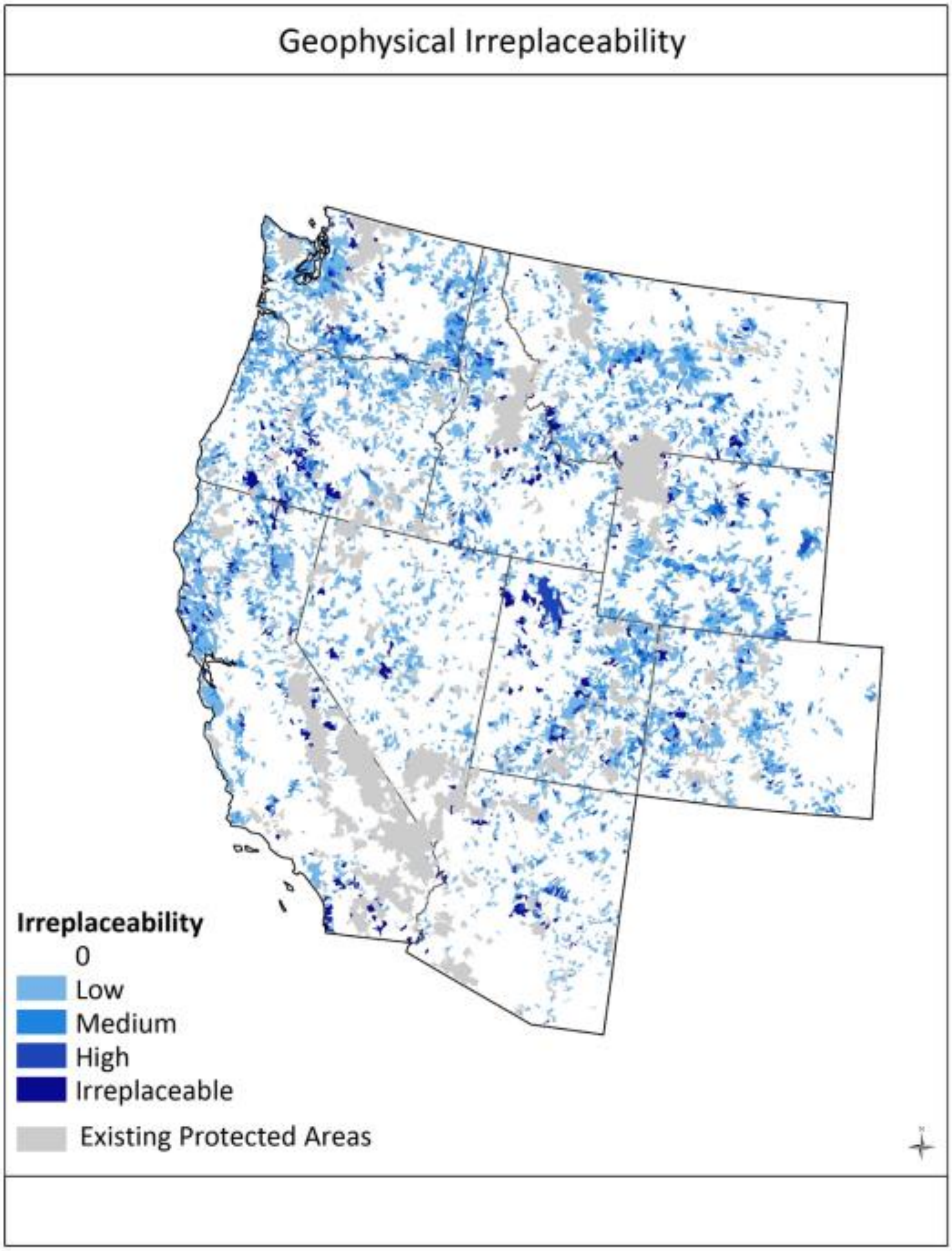


Figure 4A and 4B. Maps of irreplaceability in biological reserve networks (A) and geophysical reserve networks (B) covering approximately 16% of the study area. Irreplaceability is measured as the number of times a planning unit was selected to be in the reserve network across 100 replicates. Sites with low irreplaceability were selected in 1-32 of 100 replicates, sites with medium irreplaceability were selected in 33-66 replicates, and sites with high irreplaceability were selected in 67-100 of 100 *replicates. The biological reserve network was designed with the 250 least-common species and the geophysical reserve network was designed with the 900 least common geophysical settings.*

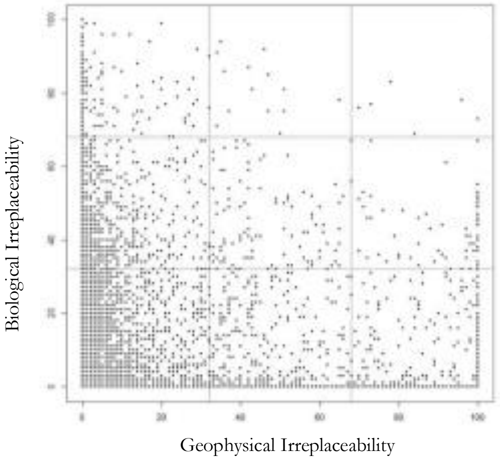


Figure 5. ***Irreplaceability of sites selected to protect current species distributions and geophysical settings.*** *Irreplaceability is measured as the number of times a planning unit was selected to be in the reserve network across 100 replicates. The biological reserve network in this plot was designed with 250 species and the geophysical reserve network was designed with 900 geophysical settings, both of which cover approximately 16% of the study area.*

In addition to the networks of sites selected based on complementarity (using Marxan) we selected sites based on richness. We found that sites selected to protect the sites with the highest species richness in each ecoregion protected slightly more species in the future than did networks selected to protect the sites richest in geophysical settings (Fig. 6). At most, the biological richness approach protected approximately 5% more species, which occurred when 20% of the landscape was covered by the reserve network. Similar to the results of the complementarity-based analyses, we found that the networks of sites selected to protect the geophysical settings performed little, if any, better than did sites selected at random. We found little overlap between high-ranking sites selected in biological and geophysical reserve networks (Fig. 7).

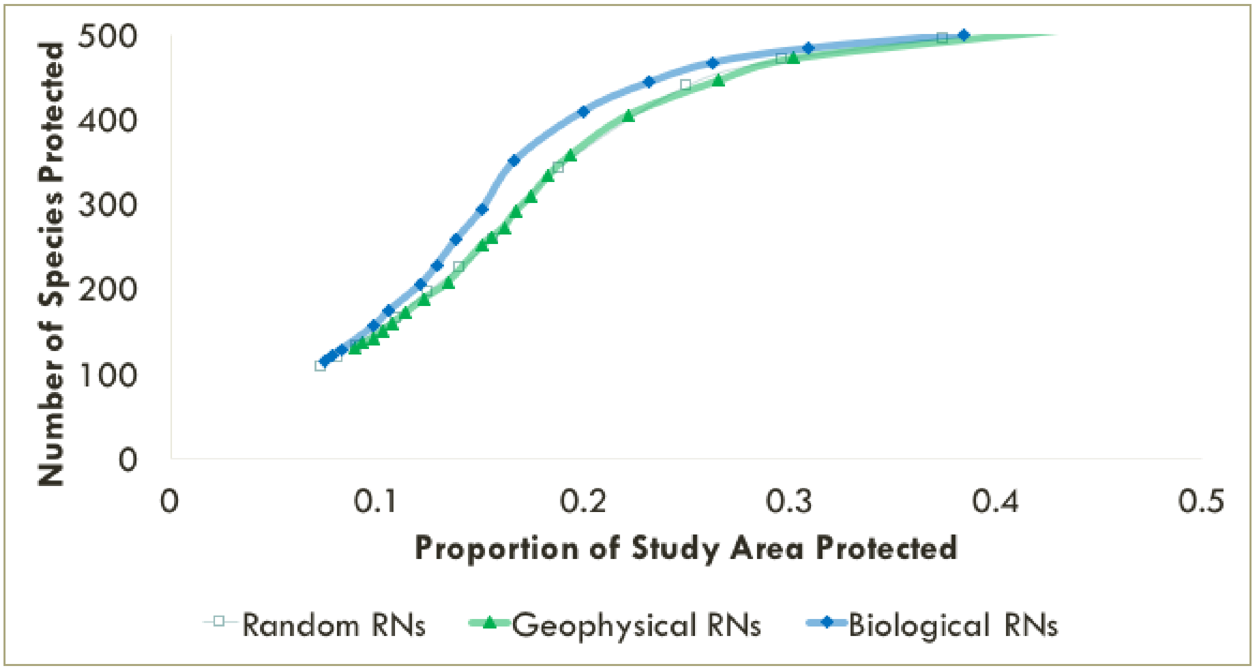


Figure 6. Results of the richness analysis using a 20% conservation feature protection target and an 50% land protection threshold per site, averaged across the 3 GCMs under the 8.5 RCP emissions scenario and in the 2070 time-period.

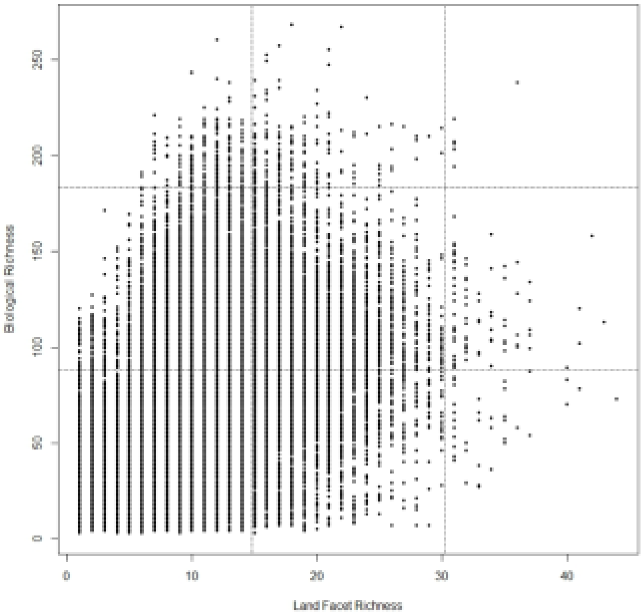


Figure 7. ***Biological and geophysical richness of sites****. Few sites are both highly biologically rich and highly geophysically rich.*

Discussion

Protecting geophysical settings is one of the most practiced approaches to selecting protected areas in the face of climate change, yet our results indicate that this approach may be little more effective than selecting sites at random. In the face of climate change, reserve networks designed based on current patterns of biodiversity are more effective at protecting future patterns of biodiversity than reserve networks designed based on geophysical diversity. The species-based reserve networks represented more species through long-term climatic changes. As the climate scenario increased in predicted change (in emissions scenario or time-period), biological reserve networks declined in effectiveness and geophysical reserve networks incrementally increased in effectiveness. However, even in the most extreme climate scenario, biological reserve networks were more effective than geophysical reserve networks. As we prepare for a climatically different future, we may protect biodiversity more successfully if we use our information on current species distributions to predict where they might occur in the future than if we turn to an abiotic proxy.

Ours is not the first study to question the effectiveness of abiotic surrogates for conservation planning. Araújo et al. (2001) demonstrated that a reserve network designed with environmental diversity poorly represented plant and animal richness in continental Europe. However, plants alone had a relatively strong relationship to environmental diversity, likely due to a greater influence of limiting environmental factors. At a smaller extent, Schloss et al. (2011) found that while sites selected to prioritize geophysical diversity successfully protected coarse vegetation types on the Columbia River Plateau, they did not adequately protect individual species. Likewise, sites selected to protect focal species poorly protect geophysical settings. Finally, a review of 622 evaluations of abiotic surrogates for species representation demonstrated that surrogates only outperformed randomly selected sites in 43% of the evaluations, and those that did, only did so by an average of 8% (Beier et al., 2015). The results improved slightly when only plant-based evaluations were considered.

The higher performance of biological reserve networks in our analysis has several potential explanations. First, perhaps biotic interactions or biotic processes are playing an important role in limiting species to specific areas and hence their distributions are not as driven by abiotic factors. For example, rare species are particularly limited by dispersal capabilities and extent, so their current distribution is likely to be a strong indicator of where they will be in the future.

Second, geophysical reserve networks at this scale are biased towards high-elevation landscapes, which may not represent species that rely on valleys or flatlands. Although species are generally expected to move higher in elevation and latitude in response to climate change, some species will not be able to reach such locations due to dispersal or environmental limitations (Chen et al., 2011; Schloss et al., 2011). Additionally, if many historical reserve networks were designated in mountainous terrain, we might expect the current protected area network to already represent a greater proportion of geophysical settings than it does species. Our results indicate that the existing reserve network already adequately (based on our 20% representation goal) represents 21.2% (226/1068) of geophysical settings compared to 17.7% (97/547) of species.

Third, reserve networks selected based on biodiversity may inadvertently capture an adequate amount of geodiversity to reap the ecological benefits of a heterogeneous environment. Using geophysical settings as a surrogate for biodiversity in conservation planning is founded on the theoretically well-established relationship between species and their environment. If this were empirically true, then current patterns of biodiversity would mirror spatial patterns of geophysical diversity and thereby one would capture the other. Although there is little empirical evidence of this intersection, even a weak correlation might add to the effectiveness of a species-based approach because it would potentially capture both the biotic and abiotic patterns of biodiversity on the landscape. Conversely, a geophysical reserve network that inadvertently captures biodiverse areas might do so less effectively because it encompasses the fundamental niche but does not consider the realized niche. That is, it captures areas that species could theoretically go, but that they have not dispersed to because of dispersal capabilities, barriers to dispersal, or other limiting factors.

The scale of our study was selected to maximize biological and geophysical relevance, while minimizing computational requirements. SDMs and geophysical settings were analyzed at a 1-km^2 resolution across the extent of the western United States. At a finer resolution—e.g., one fine enough to identify riparian zones or small, cool valleys—there may be a closer link between species' future distributions and the distribution of geophysical settings. However, in the face of climate change, broad-scale studies are important for identifying regionally imperative priorities and unifying conservation goals. Furthermore, many fine-scale refugia might be too small to support populations. Given the variable and scalable utility of geophysical settings in conservation strategies, most advocates of the approach have suggested it as complementary to the biological approach (Theobald et al., 2015; Game et al., 2011; Schloss et al., 2011; Brost and Beier, 2012; Schmitz et al., 2015; Peña et al., 2016, etc.).

Because of the magnitude of data and models that is required for these types of analyses, there are many analytical variations that could affect the outcome. Site protection threshold, species protection threshold, and climate model all had the potential to influence our results. We explored the implications of these variations and found that whereas the results did change slightly, they remained consistent and robust (see Supplemental material). In this paper, we highlighted analytical variations that represented our median results and corresponded to relevant literature. Reserve networks designed with biological targets are based on roughly 600 SDMs that reflect each species' climate envelope. They do not consider other environmental factors that influence distribution, such as soil type or land cover. The SDMs also do not directly consider biotic interactions such as competition, which may change as the climate drives dynamic changes in faunal habitat selection (Lawler et al., 2013; Beaudry et al., 2016). Nonetheless, Pearson and Dawson (2003) suggest that bioclimatic envelope modeling is the single best guide for policymaking. Araújo et al., 2005, argue that although perfect validation of climate envelope models may not be possible, such models are still useful if they are used in an appropriate context. We used the best available data and methods to carry out this test, and despite the uncertainties associated with SDMs in future climate projections, this analysis provides important insight into conservation in the face of climate change.

Conclusions

Geophysical diversity is one of the most often cited alternatives to the species-based approach in systematic conservation planning and reserve network design. The theoretical merit of geophysical diversity as a surrogate for biodiversity is well established, yet there are still uncertainties associated with predictions made based on that relationship. Those uncertainties are due to a lack of empirical evidence describing the species-environment relationship, in addition to inaccuracies in geophysical data and inconsistencies in geophysical setting classifications (Lawler and Michalak, 2017). For example, soil order and profile data can be highly uncertain across broad extents and at smaller scales, soil characteristics in relationship to individual plant species can be variable.

Given that both approaches to reserve network design presented here require some level of uncertainty, our results demonstrate that it may be more effective to prioritize conservation sites based on current species distributions rather than on geophysical settings. As climate change continues to disrupt current patterns of biodiversity, implementation of well-informed conservation strategies may reduce climate-driven loss. Future conservation plans could be enhanced by complementing the existing protected area network with sites prioritized based on projected future patterns of biodiversity. Conservation theory can provide substantial evidence in favor of strategies like the geophysical settings approach, however tests such as this are necessary to understand how the theory applies on the landscape.

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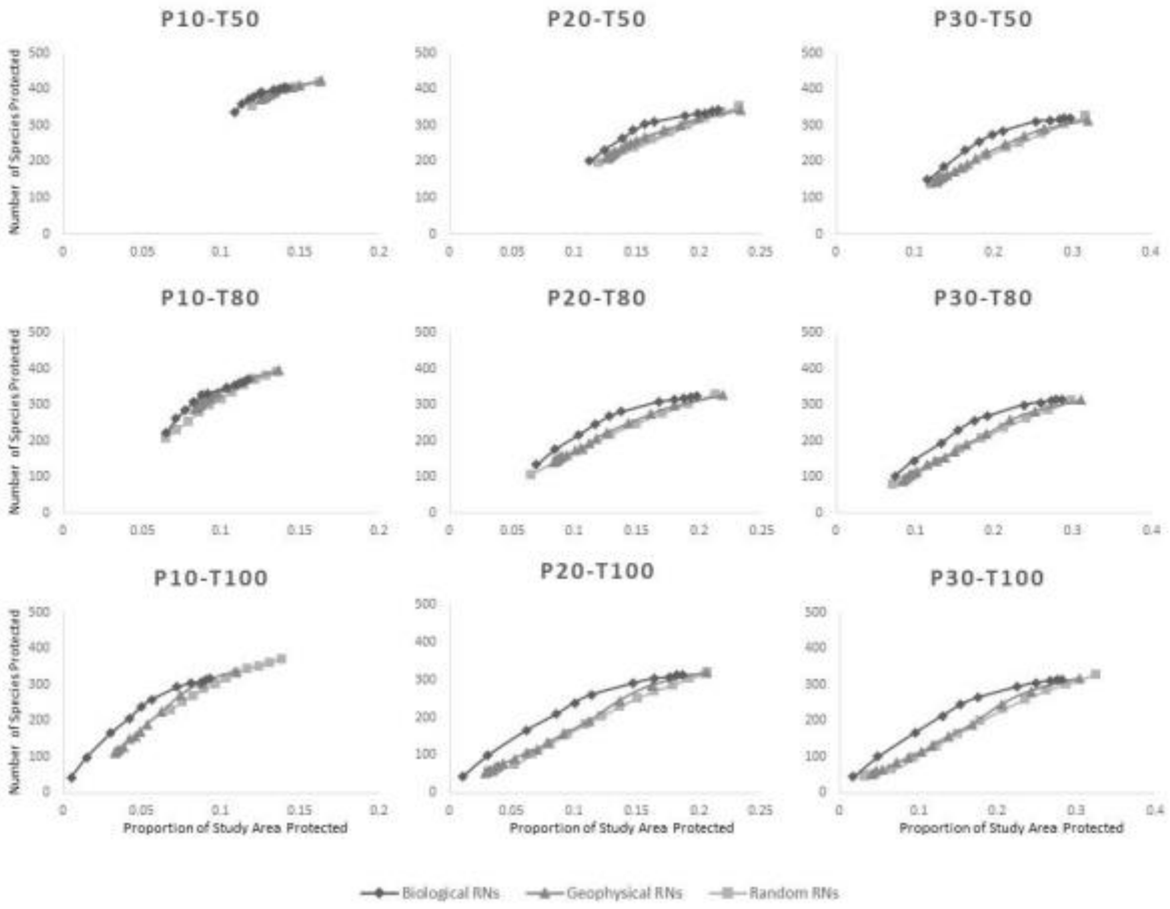
S1. Schematic of parameter variations. Each row is a variation in site protection threshold: 50% (T50), 80% (T80), and a scenario in which no site is considered already protected (T100). Each column is a variation in the amount of a species distribution that is required to be covered by the reserve network for that species to be considered protected. Variations include 10% (P10), 20% (P20), and 30% (P30).



S2. Schematic of variation in results due to climate change scenario. The first column includes results under the mildest change scenarios: INMCM4. The second column includes results under moderate change scenarios: MIROC5. The third column includes results under considerable change scenarios: GFDL-CM3.