



Selection of bioclimatically representative biological reserve systems under climate change

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Abstract

Biological reserves are intended to protect species, communities, and ecosystems in human-dominated landscapes. However, existing protected areas represent only relatively small, geographically biased samples of species and habitats. Climate change and habitat loss can exacerbate these biases and the net result is a small, skewed subset of historic environmental conditions. We developed a general model to improve the representation of environmental conditions across the range of at-risk species or any other elements targeted for conservation. We implemented the model as an integer linear-programming problem to select additional areas to complement existing reserves and create new portfolios that are bioclimatically representative across a range of climatic scenarios. We demonstrated the use of the model for a small dataset including two hydrologic variables across the range of five species of fairy shrimp (*Anostraca*) in the Central Valley ecoregion of California, USA under three climate scenarios. The bioclimatic representation model identified solutions that meet biodiversity representation goals and substantially improve bioclimatic representation at minimal additional cost in terms of total land selected for a conservation portfolio. Additional constraints rewarding bioclimatic representation under two conflicting climate scenarios resulted in only a small decrease in the performance of solutions with respect to current climate. We conclude that this model provides a general tool for improving bioclimatic representation, and results from the Central Valley case study suggest an encouraging, testable hypothesis that climatically robust bioclimatic representation can be achieved at negligible marginal costs.

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1. Introduction

Representing the diversity of environmental conditions across a region is a common objective in systematic conservation planning exercises (e.g. Faith and Walker, 1996; Noss, 2001). It has been considered a hedge against correlated population dynamics and a proxy for biological diversity (Pearson and Carroll, 1998; Garnier-Gere and Ades, 2001; Reyers et al., 2002; Ferrier, 2002; Rouget et al., 2003; Taplin and Lovett, 2003; Faith, 2003). Reserve systems that proportionally represent the diversity of regional environmental conditions have even greater importance when considered in the context of

global and regional climate change. Reserve systems are challenged to represent historic patterns of spatial and temporal variability of environmental conditions under uncertain and dynamic future conditions (Wimberly, 2002). The risk is that combinations of habitat loss and changes in the geographic distribution of climate will result in future distributions of environmental conditions that bear little resemblance to historic patterns (Keane et al., 2002). Fig. 1 demonstrates the problem with a theoretical example. In this case, we see an initial distribution of air temperature within a habitat (Curve A). A warming regional climate shifts Curve A toward higher temperatures and creates Curve B. Unfortunately, climate change is being accompanied by large-scale habitat loss. The combination of habitat loss and climate change result in a biased subset of remaining temperature conditions in this habitat represented by

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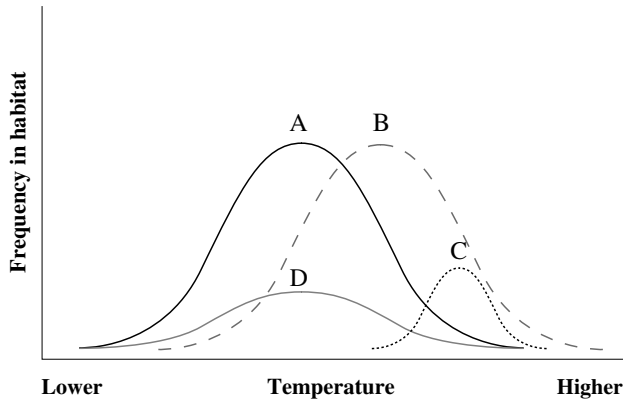


Fig. 1. Illustration of the potential impact of a combination of habitat loss and climate change on the frequency of environmental conditions in a theoretical landscape. (A) Historic distribution of temperature within a given habitat type. (B) The historic distribution is shifted toward warmer conditions under a regional climatic warming scenario. (C) A combination of habitat loss and warming result in a climatically biased sample of remaining habitat. (D) Our goal is to proportionally represent the original distribution of conditions despite an overall loss of habitat and a shift climate.

Curve C. The challenge for conservation planners is to avoid Curve C while achieving the proportional representation of environmental conditions indicated by Curve D. The loss of habitat means that Curve D is always lower than Curve A, but it is possible for it to still proportionally represent the original distribution and diversity of conditions.

These issues are relevant in many areas, since biased reserve systems are widespread. Within the United States, this is reflected in the well-known over-representation of so-called, “rocks and ice” relative to lower elevation and high productivity areas (Scott et al., 2001a,b). Biases in environmental representation can exacerbate the impacts of climate change and habitat loss (Pyke, 2004a). Repairing these biases and achieving proportional representation under present and future climate requires the strategic selection of a subset of available habitat. On-going habitat loss makes this task challenging and reduces the number of places available to maintain the full historic range and diversity of bioclimatic variation in spatial configurations that promote the persistence of sensitive biological elements (Noss et al., 1997; Wimberly et al., 2000). Rapid land-use change and delays in conservation action increase the importance of strategic habitat protection and quantitative decision support technologies (Cabeza, 2003). Unfortunately, no modeling tools are available to explicitly address the representation of environmental conditions in the context of these issues. This paper addresses these challenges by describing: (1) a generic model for incorporating environmental variability in a representation model, (2) an implementation of the model using a general-purpose integer linear program-

ming solver, and (3) a case study demonstrating the trade-offs involved in achieving environmental representation in a region undergoing a combination of habitat loss and climate change.

2. Methods

2.1. Representation models

Systematic conservation planning methods often examine the distribution of a set of conservation elements (e.g. species, communities, ecosystems) with respect to a set of planning units (e.g. watersheds, planning districts, parcels) (Pressey et al., 1993). The goal is typically to select, and then hopefully protect, a subset of planning units that maximize coverage or provide the desired level of representation for all biodiversity elements while minimizing, or at least satisfying, goals for other quantities such as cost (Camm et al., 2002; Williams et al., 2004). Once conservation elements and planning units are established, most reserve site-selection exercises utilize either element-representation (Underhill, 1994) or area-representation models (Church et al., 1996a). Ele-

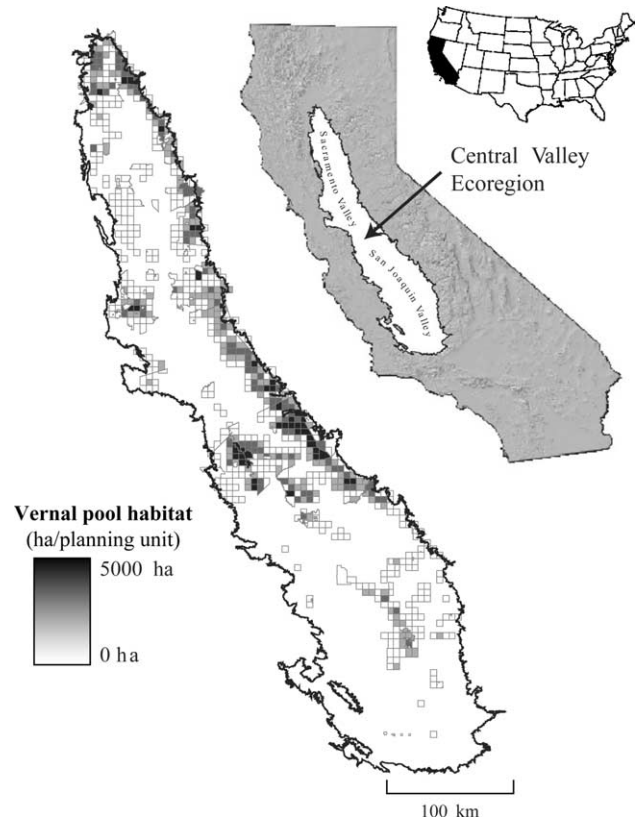


Fig. 2. The Central Valley of California, USA is divided into two sub-basins with the Sacramento Valley in the north and the San Joaquin Valley in the south. The inset illustrates the 777 planning units (CDF-FRAP, 2002). The units are shaded by their relative density of vernal pool habitat (Holland, 1998).

ment-representation models generally seek to represent a conservation element a specified number of times, based on presence/absence criteria for each planning unit. Area-based models extend the basic structure of element-based models and consider differences in the amount of habitat available for each conservation element in each planning unit. These models try to represent a specified total area of each element by selecting a subset of available planning units (e.g. Church et al., 1996b). More thorough reviews of these models are available elsewhere (ReVelle et al., 2002; Williams et al., 2004; Fischer and Church, in press).

2.2. Bioclimatic conservation elements

Both types of models have been developed and widely applied for static planning scenarios. However, in most implementations the distribution of elements is at least assumed to be well known and does not change over time. However, changes in climate and land-use introduce uncertainty into the future distribution of conservation elements and require an elaboration on these models (Cabeza, 2003). Climate change will alter the relative frequency of environmental conditions across the geographic range of each conservation element (Fig. 3). Some conditions will become more common, while others increasing rare. We hypothesize that one reasonable goal should be to preserve a subset of the original planning units that will proportionally represent the existing distribution of environmental conditions across the geographic range of each element as climate changes and habitat outside of reserves is lost. One way

that this can be accomplished is by subdividing the distribution of environmental conditions found across the range of each conservation element into multiple targets that we call bioclimatic conservation elements. The range-wide distribution of a given environmental variable (e.g., temperature, precipitation, net primary productivity, soil fertility, etc.) can be broken into an arbitrary number of bins, such as quartiles or quintiles. The amount of habitat in each bin becomes a bioclimatic conservation element that can be considered by a representation model. The goal is to use these elements to select a subset of habitat (i.e., reserves) that preserves an approximation of the original distribution of temperature conditions. There is no theoretical limit to the number of environmental variables or subdivisions that could be considered, but increasing the number environmental variables, subdivisions (i.e. bins), conservation elements, and possible reserve locations will make the problem more difficult and time consuming to solve.

2.3. Bioclimatic representation model

We developed a model to evaluate the trade-offs involved in the representation of bioclimatic elements under different climatic scenarios given limits on the total area of habitat allowed in a reserve system. The model uses a goal-programming approach that seeks to reach protection targets for each bioclimatic element and is penalized for under-protection, subject to an over-riding constraint on the maximum amount of land that could be selected for the portfolio. The reason for

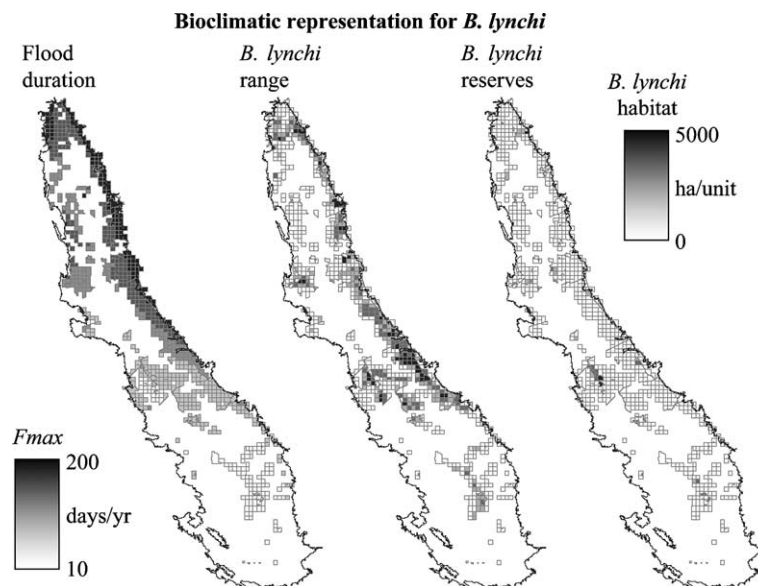


Fig. 3. Application of the bioclimatic element concept for the fairy shrimp *B. lynchi*. The three maps illustrate the geographic distributions of flood duration (F_{max}), *B. lynchi*'s known range, and reserves within its range. Notice that reserves protect a small, geographically and climatically biased subset of habitat.

using goal-programming, rather than requiring certain levels of protection, is that under some future climate scenarios certain elements may not exist and so strict protection targets would be infeasible.

Consider the following notation for the model:

k	index of a conservation element in the set K of all conservation elements
j	index of a planning unit in the set J of all available planning units
a_j	area (or cost) of planning unit j (towards area/cost limit A)
A	limit on total area (or cost) for the set of selected planning units
a_{jk}	area of conservation element k that exists in planning unit j (towards Min_k)
Min_k	minimum area of element k required in selected planning units to avoid penalty
s_k	shortfall (amount by which element k fails to reach protection target Min_k)
w_k	penalty weight for shortfall of element k in objective function
x_j	$\begin{cases} 1, & \text{if planning unit } j \text{ is selected for protection} \\ 0, & \text{otherwise} \end{cases}$

The model is defined as follows:

$$\text{Minimize : Obj} = \sum_{k \in K} w_k s_k, \quad (1)$$

Subject to:

Calculate protection shortfall for each element k based on selected units

$$\sum_{j \in J} a_{jk} x_j + s_k \geq \text{Min}_k \quad \text{for each element } k \in K. \quad (2)$$

Enforce non-negativity constraint for shortfall variables

$$s_k \geq 0 \quad \text{for each element } k \in K. \quad (3)$$

Ensure planning units selected do not exceed area (or cost) limit A

$$\sum_{j \in J} a_j x_j \leq A. \quad (4)$$

Enforce integer requirements on planning unit decision variables

$$x_j = 0 \text{ or } 1 \text{ for each planning unit } j \in J. \quad (5)$$

The objective function of the model minimizes the sum of the weighted shortfalls for each element (1). The shortfalls are calculated in constraint 2 as the difference between the target (Min_k) for each element and the protection provided by the selected planning units. The shortfalls are prohibited from being negative by constraint 3. Constraint 4 limits the total area of the selected portfolio to the pre-determined area limit A . Constraint 5 prevents planning units from being selected fractionally.

2.4. Vernal pool case study

We implemented the bioclimatic representation model for a relatively small dataset describing the distribution of fairy shrimp (*Anostraca*) with respect to two climatically sensitive hydrologic variables across the Central Valley ecoregion in California, USA. Fairy shrimp are restricted to seasonally ephemeral wetlands known as vernal pools (Holland and Griggs, 1976). The Central Valley ecoregion is a large interior basin (60,000 km²) with a Mediterranean climate and a precipitation gradient ranging from approximately 60 cm/year in the north to 15 cm/year in the south. Vernal pools remain widespread in the Central Valley, but the 3800 km² mapped in the late 1990s is believed to represent only 50% of their pre-settlement extent (Holland, 1998). Vernal pools are restricted to areas where local geomorphology and impermeable substrates combine to allow the accumulation of rain water while restricting the infiltration of water sufficiently to cause seasonal surface ponding (Hanes and Stromberg, 1998). The Central Valley's north–south climate gradient results in vernal pool hydrologic conditions ranging from over 150 days of continuous ponding per year in the northern valley to less than 10 days per year in the south (Pyke, 2002, Pyke, in press-a; Pyke, in press-b). Vernal pools have become a regional conservation issue due to a combination of an exceptional diversity of rare, endemic species and high levels of habitat loss (Holland, 1998; Vendilinski, 2000). Approximately 6.4% of vernal pool habitat remaining in the Central Valley is managed primarily for the protection of biological resources.

2.5. Planning units

The California Department of Forestry and Fire Protection has divided the Central Valley into 3211 polygons for the purposes of projecting future housing density (CDF-FRAP, 2002), and we adopted these polygons as planning units for this study. Most units are square 5 × 5 km polygons; however, some polygons are cut to conform to county and jurisdictional boundaries. The distribution of vernal pools used in this study was generated by Holland (1998) using a combination of manual air photo interpretation and ground validation. Vernal pool habitat was mapped in 777 of the CDF-FRAP polygons (median: 208 ha, mean 493 ha, SD: 662 ha), and only these units were retained in the analysis (Fig. 2). When selecting habitat for conservation, vernal pool habitat within each planning unit was either selected in its entirety or not all.

2.6. Fairy shrimp (*Anostraca*)

The biotic components of our bioclimatic elements were species of fairy shrimp (*Anostraca*). Five species

Table 1
Individual and total species area, distribution, and current levels of protection for five species of California Central Valley Fairy Shrimp

Species	Total habitat (ha)	Planning units occupied	% Of habitat in reserves
<i>B. conservatio</i>	162,525	371	5.9
<i>B. longiantenna</i>	41,350	73	26.0
<i>B. lynchi</i>	366,678	724	5.9
<i>B. mesovallensis</i>	173,468	273	2.3
<i>L. occidentalis</i>	359,682	653	5.8
All spp.	383,228	773	6.4

endemic to California were considered, including: *Branchinecta conservatio*, *B. lynchi*, *B. longiantenna*, *B. mesovallensis*, and *Linderiella occidentalis*. *B. conservatio*, *B. lynchi*, and *B. longiantenna* are currently listed under the US Endangered Species Act. These species have distinct, but overlapping ranges within the Central Valley (Eriksen and Belk, 1999). The presence or absence of each species in each planning unit was estimated by selecting all mapped vernal pool habitat (Holland, 1998) within a minimum convex polygon encompassing all published occurrences (Eriksen and Belk, 1999) (Table 1). This simple method is a compromise, and it probably over estimates the amount of occupied habitat within the delineated ranges while omitting unsampled areas outside the boundary (Worton, 1987). Specific types of vernal pools, such as northern volcanic mudflow or northern hardpan, were not identified across the range of each species. This could be done to improve the representation of climatic conditions for specific pool types, but with substantial costs in terms of the number of model constraints. For the purposes of this study, the geographic distribution of vernal pool habitat and biogeographic ranges of individual species were assumed to be fixed while the hydrologic factors were allowed to vary in response to regional climate projections (see below). These simplifications are reasonable for passively dispersed organisms in a highly fragmented environment over the next century (Schwartz et al., 2001; Higgins et al., 2003).

2.7. Hydrologic variables

The climatic components of our bioclimatic elements refer to vernal pool hydrologic characteristics. The depth, duration, and timing of inundation within vernal pools partially define the suitability of habitat for fairy shrimp maturation and reproduction (Wiggins et al., 1980; Schneider and Frost, 1996). We represented hydrologic variation across the range of each fairy shrimp species using two proxy variables: (a) the average longest continuous inundation event of the year (F_{\max}) and (b) frequency of years with flooding events ≥ 30 days (Y_{30}). F_{\max} provides an estimate of hydrologic habitat suitability, while Y_{30} provided a measure of inter-annual

variation in reproductive opportunities (i.e., the fraction of years when F_{\max} exceeds branchiopod reproductive requirements). The 30-day threshold reflects the average time required for these five fairy shrimp to reach maturity and reproduce (Helm, 1998). Longer inundations may allow greater reproduction by fairy shrimp, but they are increasingly at risk from slower-maturing, but voracious aquatic predators such as aquatic beetles, dragonflies, and amphibians (Graham, 1994; Wilcox, 2001; Brendonck et al., 2002). It is possible to implement species-specific thresholds within this model framework. However, data on this parameter are sparse, and it is very unlikely to substantially alter the results of the analysis. Although F_{\max} and Y_{30} are believed to correlate with the most important dimensions of vernal pool hydrologic suitability, many other factors may contribute to the actual occurrence of a given species. These could be added to a more elaborate implementation of this model when information suggests that their value exceeds the cost of additional model complexity.

Raster surfaces for both F_{\max} and Y_{30} hydrologic variables were available at 1 km resolution for the entire study area (Pyke, 2004a; Pyke, in press-b). These data layers indicate the predicted hydrologic response of a set of 100 rain-fed vernal pools with a range of characteristics similar to those observed for wetlands in the region (Pyke, in press-a; Pyke, 2004b). These surfaces provided spatially explicit hydrologic reference values across the region, but site-specific differences in hydrologic conditions (e.g., soil, geomorphology, etc.) need to be taken into account when evaluating the relevance of projections for any particular location. Details about the vernal pool hydrologic modeling for each variable are presented elsewhere (Pyke, 2002; Pyke, 2004b), and the data layers are available from the corresponding author.

2.8. Regional climate change

Regional climate change is projected to alter the geographic distribution of F_{\max} and Y_{30} in vernal pool habitat across the Central Valley (Pyke, 2004a; Pyke, in press-a). Despite a growing consensus regarding global climate trends, regional climate change predictions for California have differed in both magnitude and sign for key variables including temperature and precipitation (Shaw, 2003; Franco et al., 2003). A model inter-comparison found projections for 2100 ranging from slightly cooler and dryer conditions to substantially warmer and wetter conditions (Miller et al., 2001, 2003). Regional climate modeling studies have favored the higher precipitation scenarios (Nemani et al., 2001; Synder et al., 2002). It might be logical to exclusively focus on the most recent, highest resolution model projections; however, it is not credible to believe that these findings are definitive. These inter-model uncertainties are superimposed on scenario uncertainties regarding policies

and emissions and structural uncertainties regarding unrepresented features of the global climate system such as non-linear feedbacks (Stott and Kettleborough, 2002; Allen and Ingram, 2002).

Rather than attempting to select the best climate projections, this study developed methods to design reserve networks that bet-hedge between multiple, potentially conflicting climatic scenarios. For this study, we used three scenarios: (1) current/historical climate, (2) cooler, lower precipitation conditions ($-1\text{ }^{\circ}\text{C}/-10\%$ precipitation, broadly similar to the NCAR PCM), and (3) warmer, higher precipitation ($+3\text{ }^{\circ}\text{C}/+30\%$ precipitation, similar to HadCM2) (Miller et al., 2001) and regional model projections (Synder et al., 2002). Raster surfaces representing F_{\max} and Y_{30} across the study area were available for each climate change scenario (Pyke, in press-b). Values of F_{\max} and Y_{30} for each climate scenario were assigned to each of the 777 planning units, and the distribution of each variable was evaluated with respect to the distribution of the five fairy shrimp. The distribution of F_{\max} and Y_{30} across the range of each species was broken into five equal-frequency quintiles. Each of the species-by-climate quintiles became a bioclimatic conservation element (Fig. 4).

Weights were used to vary the emphasis on the individual climate scenarios by varying penalties for the under-representation of particular bioclimatic elements. These weights should reflect the relative likelihood of specific climate scenarios. Methods for assigning these values at the global scale are improving (Reilly et al., 2001; Webster et al., 2001); however, it remains difficult to assign statistically defensible and reproducible confidence intervals or probabilities to regional climate projections (Allen et al., 2001). Best current practice is to assign relative likelihood scores or “betting odds” to outcomes based on expert judgment regarding socioeconomic trajectories and biophysical uncertainty (Houghton et al., 2001). In this study, we used somewhat arbitrary weights to explore the tradeoffs involved in considering future climates during reserve selection based on bioclimatic representation. These could be easily adjusted to accommodate specific climate projections.

2.9. Equity between conservation targets

The nature of a goal-programming model is that any given solution will satisfy some goals better than other goals. In preparing a problem instance, it is important to consider which goals are the more important ones to satisfy. One ubiquitous problem in conservation datasets is balancing the conservation of the most rare and least rare elements. Consider two elements, one with a total range of 100 ha, and the other with a range of 100,000 ha. A 100 ha patch of either element would be equally favored by a strict area-based model. In order to

put first priority on conserving the rarest elements, we have implemented the model by normalizing all habitat area values as percentages of the total range of the element. Normalizing this way means that equal areas of habitat would get higher a_{jk} values for rare species than for widespread species. If area (cost) is equal, the model will tend to pick sites with higher a_{jk} values (benefit) first, until targets for the rare species are met. Analysis of data from Fischer and Church (2003) shows that this is an effective method for prioritizing the conservation of rare elements (even across much greater ranges in rarity and abundance than in our case study dataset).

2.10. Model implementation

Based on this general model, we further defined our input terms as follows. Lacking cost data for protection of each parcel of land containing habitat, we used area of vernal pool habitat within a planning unit as a proxy for cost. Area limit A is intended as a budgetary constraint, which we again approximated by limiting total area of the selected portfolio.

Given that only 6.4% of extant vernal pools are currently in reserves, we decided to investigate the possibilities of raising that percentage to 10%, 15% and 20%. This meant adding 13,809, 32,970 and 52,132 ha, respectively. Using these values for the area limit A , we initially set Min_k values the same as the percentage for A (i.e. attempt to conserve 10% of extant habitat for each element, without exceeding selection of 10% of total land area). Because this dataset shows clustering of habitat similar to many biological datasets, initial testing indicated that we could achieve significantly better total protection by setting Min_k values somewhat higher than A .

For this study we set Min_k values 10% higher than the values of A , resulting in A/Min_k pairs of 10/20, 15/25, and 20/30. For the 10/20 case, this means that we allowed a maximum of 10% of vernal pool habitat to be selected, but we continued to assess a penalty for bioclimatic elements with representation levels less than 20%. The higher value of Min_k allows the model to pick sites that encourage higher protection levels for multiple elements, at the expense of leaving fewer with lower protection levels. In other words, higher values of Min_k increase mean element protection while permitting lower equity between different elements. It is important to recall that this model minimizes the summed shortfall (with respect to Min_k) for all conservation elements, which is equivalent to minimizing the mean shortfall. This method allows relatively straight-forward comparisons between different solutions, and we will present results in terms of mean shortfall.

We ran each A/Min_k pair three times with different weights on the bioclimatic elements as described below. Comparing these runs offers insight into the tradeoffs

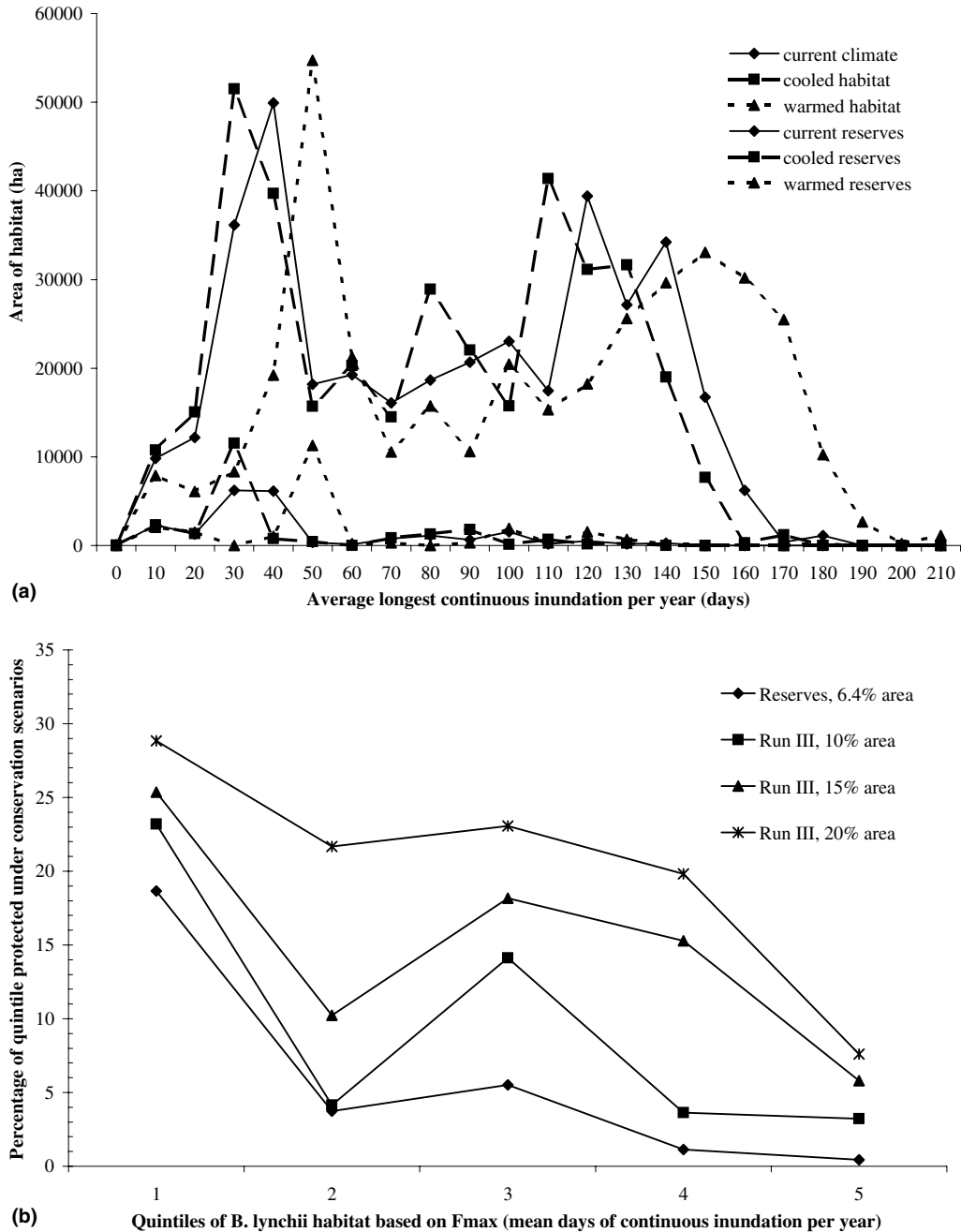


Fig. 4. The histogram (a) illustrates the distribution of F_{max} conditions within potential habitat of *B. lynchii*. Upper lines show conditions for all habitat under different climate scenarios. Lower lines show conditions just in current reserves. The current distribution is bimodal with a peak around 120 days which is not represented in reserves, and which may shift substantially under climate change. This histogram was used to create bioclimatic elements based on equal-area quintiles and (b) shows the amount of protected habitat for *B. lynchii* in current reserves, and in Run III solutions at different area limits. With increasing area limits, the solutions for *B. lynchii* get somewhat closer to a flat line (i.e. a representative sample of current climate conditions).

involved in considering current and future climate space during reserve site selection. Table 2 shows the weights used for each problem as well as solution speed and solution quality. In the following figures, the runs are marked with Roman numerals I, II, and III.

Run I did not consider current or future climate, and simply sought to meet Min_k targets for each of the five

species. This run was a goal-programming version of a traditional area-representation problem that simply attempted to increase protection for all five species without regard to bioclimatic representation.

Run II used 50 conservation elements representing the range of current conditions for F_{max} and Y_{30} (5 quintiles \times 2 hydrologic variables \times 5 species = 50 constraints). This

Table 2
Problem names, weights, and solution data

Problem name	Objective weights				Planning units selected	Solution time (s)	Gap (%)
	5 Species	50 Current climate elements	50 Cool/dry climate elements	50 Warm/wet climate elements			
Run I (10)	1.0				66	0.7	0.00
Run I (15)	1.0				48	0.6	0.01
Run I (20)	1.0				68	0.9	0.01
Run II (10)		1.0			97	1800.1	0.20
Run II (15)		1.0			89	1800.0	0.13
Run II (20)		1.0			100	1800.0	0.02
Run III (10)		1.0	0.2	0.5	116	8.3	0.01
Run III (15)		1.0	0.2	0.5	128	144.0	0.01
Run III (20)		1.0	0.2	0.5	122	462.0	0.01

Problem name shows the area limit A divided by the target level for each element Min_k , followed by a suffix to indicate which conservation elements were used. The number of planning units selected for each solution varied as shown. Problems were allowed to run until reaching a gap of 0.01% or exceeding a time of 1800 s (30 min). Gap is the difference between the objective value of the best known solution and the proven limit on possible better solutions (i.e. the lower bound), expressed as a percentage of the former.

run demonstrated the consequences of splitting individual species into bioclimatic conservation elements. This allows the model to improve bioclimatic representation at the cost of increased problem size.

Run III used the 50 conservation elements based on current hydrologic conditions, and also 50 each from the cooler/lower precipitation and warmer/higher precipitation climate scenarios. This created a problem with 150 conservation elements (3 climate scenarios \times 5 climatic quintiles \times 2 hydrologic variables \times 5 species = 150 elements). The relative priority of representation for each bioclimatic element was set by applying weights to modify the penalty associated with under-representing each element. We placed the greatest importance ($w_k = 1.0$) on representing current climate conditions, a lower weight ($w_k = 0.5$) on the warmer/higher precipitation scenario (conditions considered more likely by the climate modeling community (e.g. Synder et al., 2002), and the lowest priority ($w_k = 0.2$) on representing hydrologic conditions associated with the cooler/lower precipitation scenario. With these weights, the model would select a site that performed slightly less well at meeting current-climate goals if it improved warmer/higher precipitation climate performance by more than twice the loss of current-climate performance, or if it improved cooler/lower precipitation performance by more than five times the current-climate loss. These simple weights help us make a preliminary exploration of the trade-offs. More sophisticated methods for efficiently choosing weights might be applied in future investigations (e.g. Cohon et al., 1979; Solanki et al., 1993).

3. Computational experience

For optimization, each problem was formulated as an MPS file (a standard text file format for Linear and In-

teger Programming codes) and loaded into a general purpose Linear Integer Programming solver called CPLEX. CPLEX is a widely used, state of the art software package for linear and integer programming that utilizes a branch-and-bound process to solve mixed-integer problems like these (ILOG, 1999). Starting with a battery of heuristics, CPLEX finds a feasible solution, and then seeks to improve it or prove that it is optimal. At each step in the solution process, CPLEX tracks two numbers: the objective value of the best known solution, and the lower bound, below which it has proven no feasible solution exists. We ran CPLEX version 6.6 on a Sun Ultra SPARC 10 Station, and stopped solving when the gap between the best objective and the lower bound had closed to within 0.01% (0.0001). While a better solution is still possible, it could be no more than 0.01% better than the current solution. We also stopped CPLEX if it ran for over half an hour, regardless of the gap. Run I problems each solved to within 0.01% of optimality in less than 1 s. Run II problems (50 elements) ran for 30 min and solved to within 0.2% of optimality. Run III problems (150 elements) each solved in less than 8 min, demonstrating that underlying problem structure (i.e. large or small numbers of nearly equivalent, near-optimal solutions) can be more important than just problem size in determining solution speed. There is no theoretical limit to the number of elements in this model (provided sufficient computing power is available), but the size of the problem increases multiplicatively with the number of species, environmental variables, quantiles, and climate scenarios considered.

4. Results

4.1. Total habitat protection

The current reserve system provides uneven protection for these five species across their range of occupied

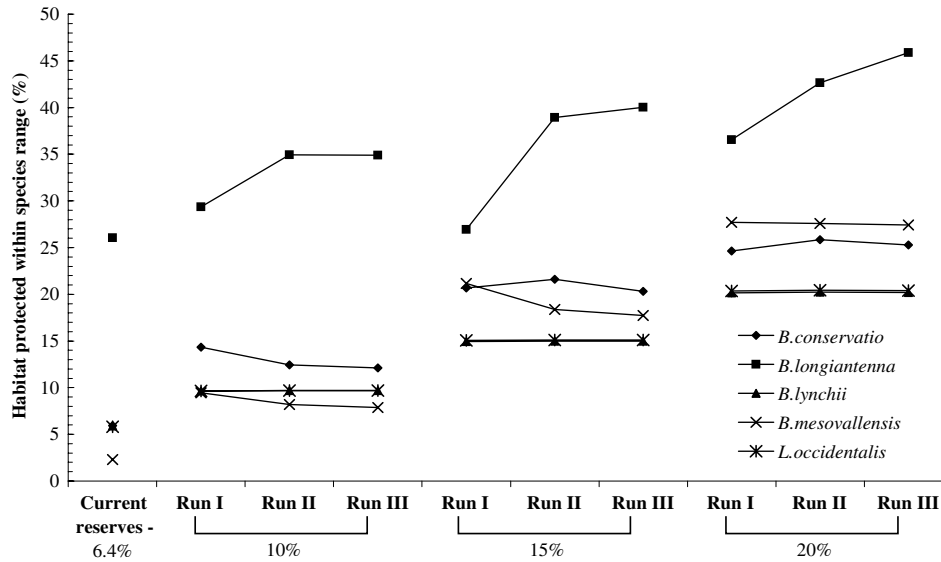


Fig. 5. The percentage of the total habitat for each species that is selected under each model run. Results for model Run I (representation-only), II (current-climate-only), and III (current and future climate scenarios) are presented as triplets for each reserve area limit (10%, 15%, and 20%). See Section 4 for details.

bioclimatic conditions. Currently, 26% of habitat within the range of *B. longiantenna* is protected while only 2% of habitat in the range of *B. mesovallensis* occurs in reserves. *B. lynchi*, *B. conservatio*, and *L. occidentalis* have about 6% of their potential habitat in reserves. The protection levels attained using all runs of the model reflect these original patterns of representation, with *B. longiantenna* receiving consistently higher levels of protection across all runs (Fig. 5). Importantly, the relative differences between species decrease as the model finds more equitable solutions.

Results for each species are presented for three prospective area limits (10%, 15%, and 20%) for each of the model formulations (Runs I–III) (Fig. 5). Each triplet of runs illustrates the trade-offs between total area protected for a species with increasingly complex consideration of climate. The best total protection achieved, without considering present or future climate conditions (Run I) followed a predictable pattern. There was substantial variance in the amount of protection achieved for different species. *B. mesovallensis*, with a moderate range, and the lowest current protection showed large improvements in protection, while *B. longiantenna*, which already met the protection target for the first two conservation levels, showed only small increases in protection. The two species with the largest ranges, *B. lynchi* and *L. occidentalis*, share the same relatively lower percentages of protection at each of the three area targets. Since *B. longiantenna* already has greater protection than 25% protection in current reserves, the additional protection provided by 10% (Run I) and 15% (Run I) models is simply the result of its co-occurrence with other species that were under-protected.

Once climate concerns were added (Runs II and III) the patterns require more interpretation. For *B. longiantenna* the drier two quintiles for both climate variables were shown to have less than 2% protection in current reserves. Repairing large shortfalls for those quintiles drove the model toward selecting significantly more total habitat for *B. longiantenna*.

With that exception, note that at a given area limit a single species receives essentially the same total percentage of its range in protected areas between all three runs (i.e. most of the triplet lines are relatively flat). The large improvements in the least represented climate elements for *B. longiantenna* in Runs II and III (and thus total protected area for that species) came at the expense of only small decreases in total protected area for *B. mesovallensis* and *B. conservatio* in the 10% and 15% solutions. This indicates that improving bioclimatic representation requires only slight, if any, increases in the total habitat area protected.

4.2. Climatic representation

We also evaluated the aggregate performance of the models for all species by climate scenario. Fig. 6 shows the mean shortfall for the groups of elements associated with each of the three climate scenarios; smaller shortfalls indicate better representation. We have considered performance for each set of 50 bioclimatic elements separately (50 current-climate elements, 50 cooler/lower precipitation elements, 50 warmer/higher precipitation elements). As described above, each of the area limits (10%, 15%, and 20%) had protection targets established 10 percentage points higher (20%, 25%, and 30%). For a

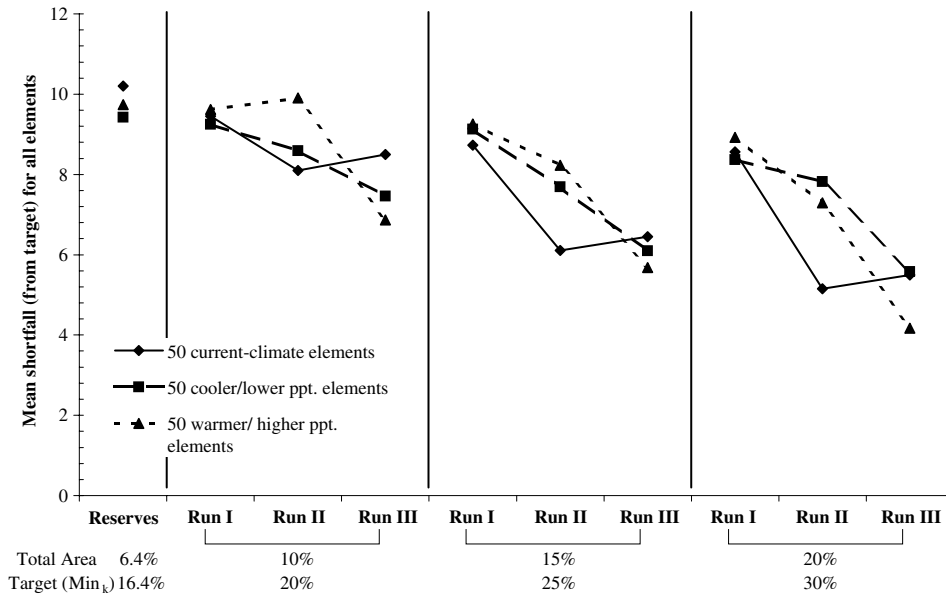


Fig. 6. Mean shortfalls for bioclimatic conservation elements, by climate scenario and by model run. Each line represents the 50 bioclimatic elements corresponding to one of three climate scenarios for a given limit on Total Area (i.e. 10%, 15%, and 20%). Run I did not consider climate. Run II considered current climate only. Run III considered all three climate scenarios. The y -axis indicates mean shortfall for all elements from the target level listed below the x -axis. For reference, the performance of the existing 6.4% reserve system was evaluated at left against a target of 16.4% yielding a shortfall of approximately 10%. See text for additional details.

benchmark, we also measured shortfalls of the current reserve system (area of 6.4%) against a target-level 10 percentage points higher (16.4%). The current reserve system logically has the highest shortfalls with respect to the targets for each bioclimatic element.

Performance for all three area limits is the worst for all climate scenarios under the Run I models. Note that mean shortfall does decline somewhat as the area limit increases (1.2% difference between current reserves and the 20% area Run I). This is due to sampling effects on clustered data and is a level of performance that could be expected from systematic reserve selection tools that do not consider bioclimatic representation.

Run III performance becomes increasingly superior to Run I performance as the threshold area and targets are increased (i.e. the triplet lines become more steeply sloped). This result indicates that the relative value of strategic selection for bioclimatic representation increases as more land is allowed into the reserve system; the larger solution sets provide increased flexibility for the model and, consequently, a wider range of better solutions.

Results for the Runs II and III models indicate that it is possible to get a much more representative sample by careful model specification and strategic additions to the existing reserve system. Run II models logically minimize shortfall for current-climate elements. In most cases, representing current bioclimatic conditions (Run II models) leads to better representation (lower shortfalls) for both future bioclimatic elements. However,

note that in the case of the 10% area limit, the Run II model actually provides worse representation under the warmer/higher precipitation scenario than the simple Run I representation model. These results indicate that representing the current distribution of conditions is a good first step, but efficient representation of future bioclimatic conditions requires additional data and explicit model structures considering future climate scenarios.

The Run III models show substantial improvements for both future climates, at relatively small costs to current-climate performance. The Runs II and III solution pairs generally have only about half their planning units in common. This suggests that there is likely a wide variety of alternate solutions with similar objective values, such that adjusting the weights applied to each climate scenario would allow a range of solutions with greater or lesser tradeoffs between the different climate scenarios. Overall, the Run III models reduced mean 150-element shortfalls by 19–41% (compared to the Run I models for the same area limits), with increasing benefit as area limits (and therefore model flexibility) increased.

5. Discussion

Climate change and habitat loss brought about by land-use change act together to change the availability of environmental conditions at regional scales. These

changes can be mitigated by the protection of environmentally representative samples of habitat in biological reserve systems. Geographic biases in the existing reserve system within the Central Valley of California create disproportionate representation of bioclimatic conditions under historic and potential future climates. Mitigating these biases should be an important component of regional conservation planning.

This study demonstrates that improvements in bioclimatic representation can be achieved with minimal costs in terms of loss of protection or reduction in the efficiency of additions to the existing reserve system. This result makes it clear that bioclimatic representation can and should be a component of systematic reserve design. It can be part of an efficient strategy to adapt to regional climate changes and preserve a representative distribution of environmental conditions. We demonstrate that substantial improvements in bioclimatic representation can be realized with the strategic protection of only 10–20% of remaining vernal pool habitat. We also show that protection without regard to bioclimatic factors will yield much less representative sets of habitat at the same cost.

We have also shown that bioclimatic analysis highlights biodiversity elements that might be overlooked in a species-centric analysis. For example, on a range-wide basis *B. conservatio* has by far the best representation in reserves. However, it turns out that existing reserves protect a biased-subset of its potentially occupied habitat. *B. conservatio*'s drier bioclimatic elements are proportionally under-protected under the current climate and this representation problem is predicted to be exacerbated under climate change. It was possible for the Runs II and III models to increase representation for these elements without compromising protection for the other species.

We demonstrated that it is possible to use climatic weights to accommodate both present and future climates at minimal trade-offs in terms of efficiency or protection equity between species. It was beyond the scope of our project to explore the full implications of varying the absolute value of these weights; however, our results suggest that it may be possible to derive a wide range of solutions with nearly equivalent area costs. This finding indicates that the careful exploration of tradeoff curves is likely to reveal significant flexibility for specific implementations. Cohon et al. (1979) offer a clear discussion of systematic methods for choosing weights to explore two-objective trade-off curves. For multiple objectives, Solanki et al. (1993) offer methods for efficiently exploring n -dimensional tradeoff curves. Either of these methods could be used to take this analysis further.

In this study, we considered three climate scenarios and divided environmental conditions for two hydrologic variables across five quintiles. These are logical but

arbitrary choices, and there is no theoretical limit to the number of possible states. Specific situations may warrant a larger or smaller number of bioclimatic elements. In addition to other factors related to climate, situations may call for the incorporation of additional environmental variables that are either static (e.g. soil type) or dynamic (e.g. disturbance history). The benefits of these increases in complexity should be carefully considered, as they may yield only small returns relative to simpler approaches focusing on dominant environmental gradients (e.g. mean annual temperature and precipitation).

An important limitation to this work is the lack of geographic information about the pre-settlement distribution of vernal pools in the Central Valley. In this paper, we go to great lengths to proportionally represent the distribution of hydrologic conditions within remaining habitat; however, the remaining pools may represent only 50% of their pre-settlement extent (Holland, 1998). The remaining 50% may represent most of the major bioclimatic features, but the relative proportions of different parts of the habitat are likely to be altered from their pre-settlement distributions (Holland, 1978; Dahl, 1990; Holland, 1998). Consequently, we run the real danger of basing our conservation targets on a shifting ecological baseline (Greenstein et al., 1998). In this case, we do the best we can with the available data, but we need to explicitly acknowledge that these baselines are partially defined by arbitrary human artifacts such as the availability of mapping or remotely sensed data. This study could also be improved by refined climate projections, more specific ecological information on the importance of different portions of the range to overall species survival, and detailed habitat-loss scenarios linked to more sophisticated models of regional land-use change including both urban and agricultural systems.

6. Conclusions

Strategic additions to existing systems of protected areas can hedge against projected future conditions at relatively modest costs in terms of additional land. A bioclimatic representation approach subdivides the distribution of environmental conditions occupied by biodiversity elements and multiplies the number of modeled conservation elements. This framework allows existing representation biases to be identified and corrected with new conservation areas that capture range-wide environmental conditions under both current and future climate. The relative emphasis on present and future is subject to weightings determined by policy-makers, analysis of uncertainty, or discounting strategies (Howarth, 2003). Our study suggests that in the Central Valley these decisions can be made with a large degree of flexibility as multiple options are available at negligible

marginal costs. There are many ways to add complexity to this basic model, but the fundamental issue is one of providing a new framework for maintaining the proportional representation of range-wide environmental conditions such that an ecological “stage” is maintained despite habitat loss and climate change.

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