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North American vegetation model for land-use planning in a changing climate: a solution to large classification problems

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Abstract. Data points intensively sampling 46 North American biomes were used to predict the geographic distribution of biomes from climate variables using the Random Forests classification tree. Techniques were incorporated to accommodate a large number of classes and to predict the future occurrence of climates beyond the contemporary climatic range of the biomes. Errors of prediction from the statistical model averaged 3.7%, but for individual biomes, ranged from 0% to 21.5%. In validating the ability of the model to identify climates without analogs, 78% of 1528 locations outside North America and 81% of land area of the Caribbean Islands were predicted to have no analogs among the 46 biomes. Biome climates were projected into the future according to low and high greenhouse gas emission scenarios of three General Circulation Models for three periods, the decades surrounding 2030, 2060, and 2090. Prominent in the projections were (1) expansion of climates suitable for the tropical dry deciduous forests of Mexico, (2) expansion of climates typifying desertscrub biomes of western USA and northern Mexico, (3) stability of climates typifying the evergreen–deciduous forests of eastern USA, and (4) northward expansion of climates suited to temperate forests, Great Plains grasslands, and montane forests to the detriment of taiga and tundra climates. Maps indicating either poor agreement among projections or climates without contemporary analogs identify geographic areas where land management programs would be most equivocal. Concentrating efforts and resources where projections are more certain can assure land managers a greater likelihood of success.

Key words: climate change impacts; climate niche modeling; land management alternatives; Random Forests classification tree; vegetation models.

Introduction

Global climate change during the last 50 years has begun to alter natural ecosystems (see Soja et al. 2007). Species distributions are being affected at their trailing edges by dieback and mortality in *Populus tremuloides* (Worrall et al. 2008, Rehfeldt et al. 2009, Michaelian et al. 2011), *Pinus ponderosa* (Gitlin et al. 2006), and *Pinus edulis* (Shaw et al. 2005, Breshears et al. 2005) in North America and for an additional 88 tree species worldwide (Allen et al. 2010). Migration is also well documented at the leading edge in North America (Woodall et al. 2009), Europe (Jump et al. 2009), and Siberia (Tchebakova et al. 2010). Dieback and mortality of *Abies religiosa* (C. Sáenz-Romero, *personal communication*) in Mexico is reducing habitat for the monarch butterfly in its winter refuge, as predicted by the models of Oberhauser and Peterson (2003). Yet, the largest and most rapidly spreading climate-induced ecosystem changes involve insect outbreaks, either directly in response to climate anomalies (Candau and Fleming 2005, Carroll et al. 2006, Berg et al. 2006, Gray 2008, Raffa et al. 2008) or indirectly on trees weakened by moisture stress (Negrón et al. 2009, Ganey and Vojta 2010). Such climate-induced impacts when combined with altered wildfire frequencies (e.g., Flannigan et al. 2009, Tchebakova et al. 2009) are expected to drive vegetation change and alter species assemblages, shift ecological zones, and generate new ones.

Land managers require decision-support tools suitable for dealing with oncoming climate-mediated ecosystem changes. Progress has been made in converting climatically static vegetation simulators to climatically dynamic models (see Crookston et al. 2010), and guidelines are in use for managing future generations of the broadly dispersed *Larix occidentalis* (Rehfeldt and Jaquish 2010) of western North America and the narrow endemics, *Picea chihuahuensis*, *P. mexicana*, and *P. martinezii* of Mexico (Ledig et al. 2010). Yet, for much of North America, comprehensive management guidelines do not exist. Our goal was to develop a statistically valid, climate-driven vegetation model suitable for land-use planning during a changing climate.

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Because General Circulation Models (GCM) are key to understanding future climates, the tool we envision must take into account the variability in GCM output resulting from different model formulations and emissions scenarios. However, to land managers, variation represents uncertainty, and uncertainty often leads to inaction. Our approach was to emphasize similarities in responses projected from the disparate formulations rather than dwell on the differences. The tool must also contain provisions for identifying future climates with no contemporary analog (see Williams and Jackson 2007, Williams et al. 2007) because new climates may best be suited for species assemblages that do not exist today (see Jackson and Overpeck 2000, Ackerly 2003). To be useful, the scope of a vegetation model should be neither too broad (e.g., Monserud et al. 1993, Cramer et al. 2001) to constrain local interpretation nor so parochial (e.g., Hamann and Wang 2006, Rehfeldt et al. 2006, Schneider et al. 2009) as to limit management options. It is mandatory, moreover, that this tool incorporates powerful statistical techniques that retain the robustness and flexibility necessary for anticipating and accommodating actual changes.

Our analysis uses the biotic communities of Brown (1994), mapped and digitized by Brown et al. (1998). This classification system meshes well with our goals: It is based on distributions of flora and fauna without reliance on physiography, the coverage includes all of North America, and altitudinal zonation of vegetation is an integral part of the system. For simplicity, we use the term "biome" to reference the biotic communities. Previous analyses (Rehfeldt et al. 2006) used this classification system for modeling climatic control of biome distributions in western USA. These analyses produced errors of fit ($\approx$10%) that largely resulted from an imperfect alignment between digitized polygons in the classification system and the digital elevation model (DEM; GLOBE Task Team 1999) used to generate point estimates of biome climates. Misalignment had greatest impact at borders of polygons, along shore lines, and on mountain peaks, and therefore, was of greatest source of error with small, irregularly shaped polygons and for biomes occurring in altitudinal sequence. In this analysis, we considered biomes from throughout North America (latitude $> 13.9°$ N) and used supplemental information to alleviate adverse effects of the misaligned data files.

We built on the statistical modeling of Rehfeldt et al. (2006) to predict contemporary realized climatic niches of North American biomes. Ecological niche models have received considerable criticism (e.g., Hampe 2004, Jackson et al. 2009) mostly because of their inability to represent migration or colonization potentials, competitive interactions, and effects of enhanced CO_2 on water-use efficiency. The first of these is not an issue. Niche modelers themselves make no claims of projecting species distributions, but instead emphasize that their models project suitable climates (e.g., Rehfeldt et al. 2006, Iverson et al. 2008). Likewise, competitive interactions that limit species distributions can be defined climatically and are invalidated only when future climates have no contemporary analog. By predicting and projecting the occurrence of novel climates, statistical models can negate this second point of contention. However, it is true that correlative models are not yet capable of accounting for physiological impacts of enhanced CO_2 on gas exchange and productivity. Such effects, however, are well characterized in only a few species, and impacts on species distributions are unknown (John Marshall, University of Idaho, *personal communication*). More research is required before effects of enhanced CO_2 can be incorporated with credibility into vegetation models (see Bachelet et al. 2008), whether correlative or mechanistic.

Methods

Data acquisition

The classification of Brown et al. (1998) contains 82 biomes and 5707 polygons for North America. We used five steps to assemble a data set (see Appendix A for details): (1) extract data points from each polygon, (2) assign an elevation to each data point, (3) reduce the number of classes by combining similar biomes and eliminating those superfluous to our objectives, (4) use supplementary data to address issues concerning misalignment between biome digitization and the DEMs of GLOBE Task Team (1999), and (5) obtain climate estimates for each data point from spline climate surfaces (*available online*).[5] The resulting database had about 1.75 million observations spread across 46 biomes (Table 1). In the text and figures to follow, biome names are followed in parentheses by the number of that biome coded in Table 1; the number is also the key to color chips in the figures.

Statistical procedures

We used the Randon Forests classification tree of Breiman (2001), available in R (R Development Core Team 2004), to develop a statistical model predicting the distribution of biomes for the contemporary climate. In the vernacular this algorithm uses, random procedures are used to build numerous "trees" within one or more "forests." Predictions are made according to "votes" cast by each "tree," which, in our case, would pertain to which biome the climate of an observation would be suited. The algorithm in R, however, limits the number of classes to 32. To circumvent this limitation while incorporating a method for identifying climates without analogs, we used 100 "forests," each containing observations from nine biomes plus an additional class containing a sample of observations from the remaining 37 biomes. Our intention for the latter class, coded as biome 99, was for it to collect observations having no climatic analog among the 46 North American biomes

[5] http://forest.moscowfsl.wsu.edu/climate/

TABLE 1. Biome names, codes, their relationship to the biotic communities of Brown et al. (1998), and area occupied, number of data points available for analysis, the number of "forests" in which that biome was used to develop a bioclimate model from the Random Forests algorithm, and errors of prediction from that model.

Code	Biome name	Biotic community of Brown et al. (1998)	Area (thousands of km^2)	No. data points (in thousands)	No. "forests"	Error of prediction (%)†
Primarily in Mexico						
1	Gulf Coast Thornscrub	3134300	188.0	8.3	21	1.1
2	Transvolcanic-Guatemalan Conifer Forest	1122101, 1122900	10.3	7.4	18	0.1
3	Sinaloa Dry Deciduous Forest	3124104, 3124106	72.9	9.8	19	1.2
4	Guerrero-Guatemala Dry Deciduous Forest	3124400, 3124900	154.5‡	19.1	16	0.5
6	Interior Chaparral	1133300, 1133400	40.9	21.3	20	0.3
10	Madrean Montane Conifer Forest	1122800	37.0	7.9	11	0.1
11	Yucatan Dry Deciduous Forest	3124800	24.3	4.0	17	0.1
12	San Lucas Pine–Oak Woodland	1123101	1.2	3.9	19	0.5
17	Guerrero-Guatemala Evergreen (Oak) Woodland	1123600, 1123800	108.1‡	33.0	21	3.8
18	Savanna Grassland	3144100, 3144200, 3144300	86.6‡	19.3	12	0.4
19	Tropical Semi-evergreen Forest	3124103, 3124300, 3124102, 3124600	207.2‡	32.0	19	4.5
26	Yucatan-Tamaulipas Semi-deciduous Forest	3124105, 3124700	54.0	15.6	12	0.4
27	Cloud Forest	1123700, 1123900	20.8‡	11.1	19	0.0
28	Tropical Rain Forest	3124101, 3124200, 3124500	274.5‡	19.7	12	1.1
33	Madrean-Transvolcanic Pine–Oak Woodland	1123300, 1123500	274.6	52.9	23	14.3
34	Sinaloa-Guerrero Thornscrub	3134100, 3134200, 3134400	104.5	18.1	19	0.5
35	Sonoran Desertscrub	3154100	305.6	13.8	26	0.6
39	Chihuahuan Desertscrub	1153200	380.1	18.3	22	0.3
40	Semidesert Grassland	1143100	507.8	57.9	22	15.4
Primarily conterminous United States						
7	Great Basin Montane Scrub	1132100	28.5	15.1	19	0.2
8	Great Basin Conifer Woodland	1122700	297.8	102.8	17	21.5
9	California Chaparral	1133100	33.6	13.0	21	0.6
14	Oregon Deciduous and Evergreen Forest	1122400	36.5	10.2	18	0.1
15	Gulf Coastal Grassland	1143300	51.9	7.7	20	0.1
20	California Evergreen Forest and Woodland	1123200	62.4	11.2	16	1.8
21	Cascade-Sierran Subalpine Conifer Forest	1121400	55.1	18.7	18	0.4
23	California Valley Grassland	1143200	71.4	11.1	16	0.9
24	California Coastalscrub	1133200	26.7	4.2	23	0.2
25	Interior Cedar–Hemlock Forest	not classified	111.2	46.6	25	2.8
29	Eastern Deciduous and Evergreen Forest	1123100	629.9	39.0	22	0.6
30	Mohave Desertscrub	1153100	124.0	7.5	23	0.5
31	Oregon Coastal Conifer Forest	1122300	123.8	9.4	25	0.1
32	Cascade-Sierran Montane Conifer Forest	1122500	149.0	14.6	22	1.5
37	Eastern Subalpine Forest and Tundra	1111800, 1121500	17.5	15.3	17	0.0
38	Great Basin Desertscrub	1152100	331.9	36.3	12	9.8
42	Great Basin Shrub–Grassland	1142200	523.8	46.2	20	8.8
43	Rocky Mountain Montane Conifer Forest	1122600	443.0	75.8	26	13.1
47	Great Plains Grassland	1142100	2341.5	100.4	31	4.4
48	Temperate Deciduous Forest	1122100	2712.0	39.4	16	7.3
Primarily Canada and Alaska						
22	Western Alpine Tundra	1111600, 1111700, 1111900	56.2	24.7	26	0.3
36	Coastal Hemlock Forest	1122200	209.0	80.7	23	3.1
41	Rocky Mountain Subalpine Conifer Forest	1121300	396.9	111.8	26	17.9
44	Alaska Alpine Tundra	1111500	482.0	124.0	12	14.2
45	Arctic Tundra	1111100, 1111200, 1111300	2843.4	250.4	16	4.6
46	Alaska Subarctic Conifer Forest	1121100	919.3	54.0	19	1.8
50	Canadian Taiga	1121200	4631.2	103.7	16	7.1

Note: The bioclimate model was developed with the Random Forests classification tree using 100 "forests" each with 100 "trees."
† Overall error was 3.7%.
‡ Truncated at 13.9° N latitude.

we used. Only 10 classes were used per "forest" because Random Forests uses a random selection of classes to split nodes when there are >10 classes.

In our programming, predictions are made according to the average of the "votes" cast in those "forests" within which a biome occurred. For instance, to predict the biome suited to a data point, the number of "votes" in favor of the climate being suited to biome 1 would be the average of "votes" given biome 1 from the 21 "forests" (see Table 1) within which biome 1 occurred; that for biome 2 would be the average of "votes" from the 18 "forests" in which biome 2 occurred; and that for biome 99 would be the average "votes" from the 100 "forests." The prediction, then, would be the biome with the largest average.

Nine biomes were allocated to the 100 "forests" according to three procedures. For 16 "forests," biomes were selected by us to assure that regionally proximal biomes would occur together in at least one "forest." The eighth "forest," for instance, contained biomes 7, 8, 22, 30, 38, 41, 42, 43, and 47, all of which can occur in altitudinal sequences in the interior West of the United States. For 50 "forests," a random sample of nine biomes was taken within one of three regional groupings: For 11 of the 50, nine biomes were drawn at random from the 16 having all or a portion of their distributions at latitudes north of 45° N; for 20, the nine biomes randomly sampled the 29 biomes having a portion of their distribution between 45° N and 30° N; and for 19, the nine came from the 26 biomes with distributions south of 30° N. For the remaining 34 "forests," nine biomes were drawn at random from the pool of 46. This procedure assured that at least two-thirds of the "forests" would contain biomes most difficult to separate.

To provide a reasonable balance of observations representing the biomes in a "forest" (see Breiman 2001), each biome was limited to a maximum of 20 000 observations randomly drawn from the database. This limit meant that all observations for about one-half of the biomes would be included in all "forests" containing that biome (see Table 1). Biome 99 was represented by a random sample of 555 observations from each of the 37 biomes not in the "forest."

The sampling procedure produced 100 data sets containing at least 130 000, but no more than 200 000, observations. Each data set was run through the Random Forests algorithm using 100 "trees" and 34 climate variables (see Rehfeldt et al. 2006) for predictors. A stepwise elimination procedure was used, that is, the algorithm was run with the full complement of predictors; variable importance was judged according to the mean decrease in accuracy averaged for each variable across all "forests"; variable(s) were culled; and the algorithm was re-run with the new complement of predictors. The five least important climate variables were eliminated in the first step, but, thereafter, one variable was removed at each step until 15 variables remained.

Interpreting statistical output

The Random Forests algorithm calculates an out-of-bag error for each "forest." Because we used a sample of biomes for each "forest," out-of-bag errors in our analyses depend on which biomes were being compared. To obtain a realistic estimate of the statistical fit of the model, 10 data sets were drawn from the database, each containing a random sample of 2000 observations for each biome. Each data set was run through the 100 "forests" to estimate errors of prediction.

To judge the effectiveness of our procedures for identifying climates having no analogs within North American biomes, we assembled a data set of worldwide climates for locations beyond North America from the U.S. Department of Commerce, NOAA Satallite and Information Service, National Climate Data Center (*available online*).[6] Of the data available, the derived variables of Rehfeldt (2006) could be calculated for 1528 locations. These observations were run through the classification tree to predict for which North American biome their climate would be analogous. Our assumption was that a high proportion of worldwide climates should have no analogs among the 46 biomes and that they would be identified when biome 99 was the prediction.

Mapping projections

We used climate grids (*available online*; see footnote 5) made by feeding GLOBE Task Team's (1999) DEMs (0.0083° resolution) of North America through spline temperature and precipitation surfaces (see Rehfeldt 2006, Saenz-Romero et al. 2010) and calculating derived variables (Rehfeldt 2006) of demonstrated utility in biogeography. Also available from this website are climate grids projected into future climate space for two greenhouse gas emissions scenarios of three General Circulation Models (GCM): (1) Canadian Center for Climate Modelling and Analysis, using CGCM3 (T63 resolution), SRES A2, and B1 emissions scenarios; (2) Met Office, Hadley Centre, using HadCM3 and emission scenarios SRES A2 and B2; and (3) Geophysical Fluid Dynamics Laboratory, using CM2.1 and emissions scenarios SRES A2 and B1. Description of the data sets and an explanation of the scenarios are *available online* at the International Panel on Climate Change Data Distribution Center.[7] In general, the A2 scenario represents continued high greenhouse gas emissions, while the B1 and B2 scenarios incorporate social and economic restraints on emissions.

Procedures used for downscaling the coarse GCM grids; updating contemporary climate records; fitting

[6] http://www.ncdc.noaa.gov/oa/climate/ghcn-monthly/index.php

[7] http://www.ipcc-data.org/

Table 2. Ecotones and altitudinal sequences of biomes contributing most prominently to classification errors.

Vegetation transitions	Inclusive biomes†	No. errors	Percentage of total error‡
Rocky Mountain altitudinal sequence	38, 7, 8, 43, 41, 22, 42, 25, 40	11 359	33.7
Great Plains ecotones	47, 8, 48, 43, 40, 50	2076	6.2
Subtropical woodlands	33, 2, 3, 4, 6, 10, 34, 39, 40	5137	15.2
Tropical	19, 17, 26, 27, 28, 33	1098	3.3
Arctic ecotones	44, 22, 36, 41, 45, 46, 50	7210	21.4

† Biome numbers keyed to Table 1.
‡ Total error was 33 700 observations.

new spline surfaces for future climates; and developing grids from GLOBE DEMs for three time periods, the decades surrounding 2030 (i.e., 2026–2035), 2060, and 2090 are documented elsewhere (Rehfeldt et al. 2006, Saenz-Romero et al. 2010).

Grids of future climates were run through the Random Forests classification tree to project future distributions of realized climate niches of the 46 biomes. Sets of maps were produced with and without predictions for biome 99, the no-analog classification. For the former, biomes were assigned to grid cells according to the plurality of the voting, ignoring the votes given to biome 99. Maps of those grid cells for which biome 99 received the plurality were used as overlays on maps predicting and projecting the geographic distribution of actual biomes.

In mapping, we adopted the view of Hansen et al. (2001, but see also Rehfeldt et al. 2009, Rehfeldt and Jaquish 2010, and Ledig et al. 2010) that GCM and scenario output represent a continuous range of potential impacts. Disagreement among projections is viewed as uncertainty. Adopting this view allowed us to emphasize similarities among projections without completely subjugating the well-established differences between GCMs and scenarios. To that end, we mapped the consensus among the six projections at each time slice; that is, biomes were assigned to grid cells according to which biome received the plurality of the six predictions; ties were settled randomly. We also mapped uncertainty by superimposing the six projections and mapping for each pixel the number of projections that agree with the plurality. When three or fewer projections agree, we assumed that uncertainty is high; that is, two-thirds of the projections must agree before confidence is placed in a prediction. Using this threshold meant that a prediction of reasonably high likelihood would require some agreement between low- and high-emissions scenarios. Predictions of future climates without contemporary analogs also were identified by agreement among two-thirds of the projections. Ensuing recommendations are based, consequently, on predictions robustly suited to a broad range of future climates.

Results

Classification tree

Out-of-bag errors arising from the model-building process averaged 5.4% across the 100 "forests," ranging from 2.1% to 10.3%. Errors averaged 7.9% in the 16 "forests" containing proximal biomes, 5.3% for those in which biomes were selected at random within geographic subregions, and 4.6% for those in which biomes were selected at random from throughout North America.

The overall classification error obtained from 10 samples of 2000 observations from each biome averaged 3.7%, but was as high as 21.5% (Table 2) for the Great Basin Conifer Woodland (biome 8; Table 1). Most of the error involving this biome resulted from confusion among biomes 7, 38, 42, and 43, all of which tend to occur proximal to biome 8. All are part of Great Basin and Rocky Mountain altitudinal sequences, which in total accounted for 33.7% of the misclassified observations (Table 2). Vegetation transitions in the arctic and in tropical forests were secondary contributors to classification error (Table 2).

Of 1528 observations from beyond North America, 22.8% had climates predicted to be analogous to those of the North American biomes (Table 3). Most notable were (1) the high proportion of observations from Asiatic Russia having analogs with Canadian Taiga and Great Plains Grassland; (2) Australian climates having analogs with nine North American biomes, particularly with the Sonoran Desert, thornscrubs, and woodlands of Mexico; (3) the large number of analogs in China for the Great Plains Grassland; (4) analogs of the temperate deciduous forests in Japan; and (5) the lack of North American analogs for climates of Ireland, Pacific Islands, and Indian Ocean Islands.

Mapped predictions and projections

Biome areas predicted for the contemporary climate (Fig. 1, Table 4) correlated nearly perfectly ($r = 0.9975$) with those digitized by Brown et al. (1998), even though biome 25 was not in the original classification. The classification tree captured the complex spatial transitions among the major vegetation units of British Columbia, Canada (Fig. 2a): from maritime to continental in the south, montane to alpine tundra in the Coastal and Rocky Mountains, and temperate to arctic in the north. At a finer scale, Fig. 2b illustrates biome transitions encompassing the Uinta Range in Utah, USA: from alpine tundra (22) to subalpine conifer (43) and montane conifer in the mountains, to montane scrub on the west (7), shrub–grassland (42) to the north, and desertscrub (38) to the south.

TABLE 3. Summary of climatic analogs to North American biomes for 1528 worldwide locations.

Country or region	No. data points	Percentage analogous	No. analogous biomes†	Most common analogous biomes‡
Iceland-Greenland	2	50.0	1	Arctic Tundra (1)
Antarctica	4	50.0	1	Arctic Tundra (2)
Asiatic Russia	99	43.4	6	Canadian Taiga (25) Plains Grassland (7)
South Africa	26	38.5	8	Madrean Pine–Oak Woodland (10)
Northern Europe	71	38.0	6	Rocky Mountain Montane Forest (21)
Northern Africa	30	33.3	6	Sonoran Desertscrub (3)
Turkey-Armenia-Georgia	57	28.1	5	Great Basin Shrub–Grassland (11)
Japan	48	27.1	1	Temperate Deciduous Forest (13)
Australia	359	25.1	9	Sonoran Desertscrub (35) Madrean Pine–Oak Woodland (17) Pacific Coast Thornscrub (11)
Southeast Asia	33	24.2	3	Interior Chaparral (3)
China	353	23.8	7	Plains Grassland (68)
Indian Subcontinent	65	16.9	6	Sonoran Desertscrub (6)
Caribbean Islands	49	16.3	4	Tropical Semi-evergreen Forest (3)
Hawaii	29	13.7	1	Tropical Rain Forest (4)
Southern Eurasia	36	11.1	2	Plains Grassland (3)
Southern Europe	87	5.7	4	Great Basin Shrub–Grassland (2)
South Korea	28	3.5	1	Temperate Deciduous Forest (1)
Philippines-Indonesia	105	1.9	1	Tropical Rain Forest (2)
Pacific Islands	33	0.0	0	
Indian Ocean Islands	3	0.0	0	
Ireland	11	0.0	0	

† Overall percent analogous was 22.2%.
‡ The numbers in parentheses indicate the number of times that the biome was predicted to be a climatic analog to a weather station in the country listed.

Impacts of low- (B) and high- (A) emissions scenarios were similar for the decade surrounding 2030 when the absolute value of change in area averaged 34% for A scenarios and 36% for the B. For the decade surrounding 2060, the average change was 58% for the A scenarios and 47% for the B, and for 2090, 78% for the A and 61% for the B. However, when impacts to a single biome are considered (Fig. 3), effects of the emissions scenarios are obscured until late in the century by variation attributable to the GCMs. Albeit, biome 8 was chosen for Fig. 3 because of the consistent temporal impacts to this biome estimated across the century (Table 4), but the obvious conclusion is that the effect of emissions scenarios depends on the GCM used. Fig. 3 also illustrates the importance of providing land managers robust guidelines that take into account uncertainty about future conditions. To this end, disparate projections can be considered as a continuous range of responses along similar trajectories, with differences among projections being largely temporal (see also Rehfeldt et al. 2009, Rehfeldt and Jaquish 2010). That is, the projections tend to follow the same paths but differ in the time when the same amount of impact is reached.

To uncover commonalities beneath the variation, we first considered impact as temporal ensembles (Table 4) and mapped the consensus of the projections (Fig. 4). Most obvious for Mexico are increases in area suitable for biomes of arid climates: the tropical dry deciduous forests (3, 4, and 11), thornscrubs (1 and 34), and the Sonoran Desertscrub (35). These increases would be largely at the expense of climates suitable for conifer forests (2 and 10), semi-deciduous forests (26), and cloud forests (27). Significant findings for the United States include the expansion of climates suited to the arid scrublands of the West (7, 30, 35, and 38); loss of climates suited to subalpine conifer forests (21, 37, and 41) and alpine tundra (22); lack of change in the distribution of climates suited to the Great Plains Grassland (47), temperate deciduous forests (48), and deciduous–evergreen forests (29). For Canada, losses of climates suited to alpine tundra (22 and 44), arctic tundra (45), and taiga (50) would result from northward and expansion of climates suited to more southerly biomes (e.g., 25, 47, and 48). Also apparent, but of obscure relevance to either ecology or management, is the gradual insinuation of climates typical of subarctic conifer forest (46) between those of taiga (50) and arctic tundra (45) (Fig. 4b–d). Trailing edge impacts are addressed in detail in Appendix B for four biomes selected to illustrate the complexity of projected responses.

Impact can be further quantified by the proportion of the contemporary niche that remains constant in time (Table 4). On average, by 2030, 72% of the grid cells in the North American map should have climates suitable to the biomes that occur there today; by 2060, the percentage drops to 62%, and by 2090, to 56%. When averaged across GCM formulations, emissions scenarios, incidentally, differed by only 1% in the amount of contemporary niche remaining constant in 2030, by 4% for 2060, and by 14% for 2090. Biomes that do not

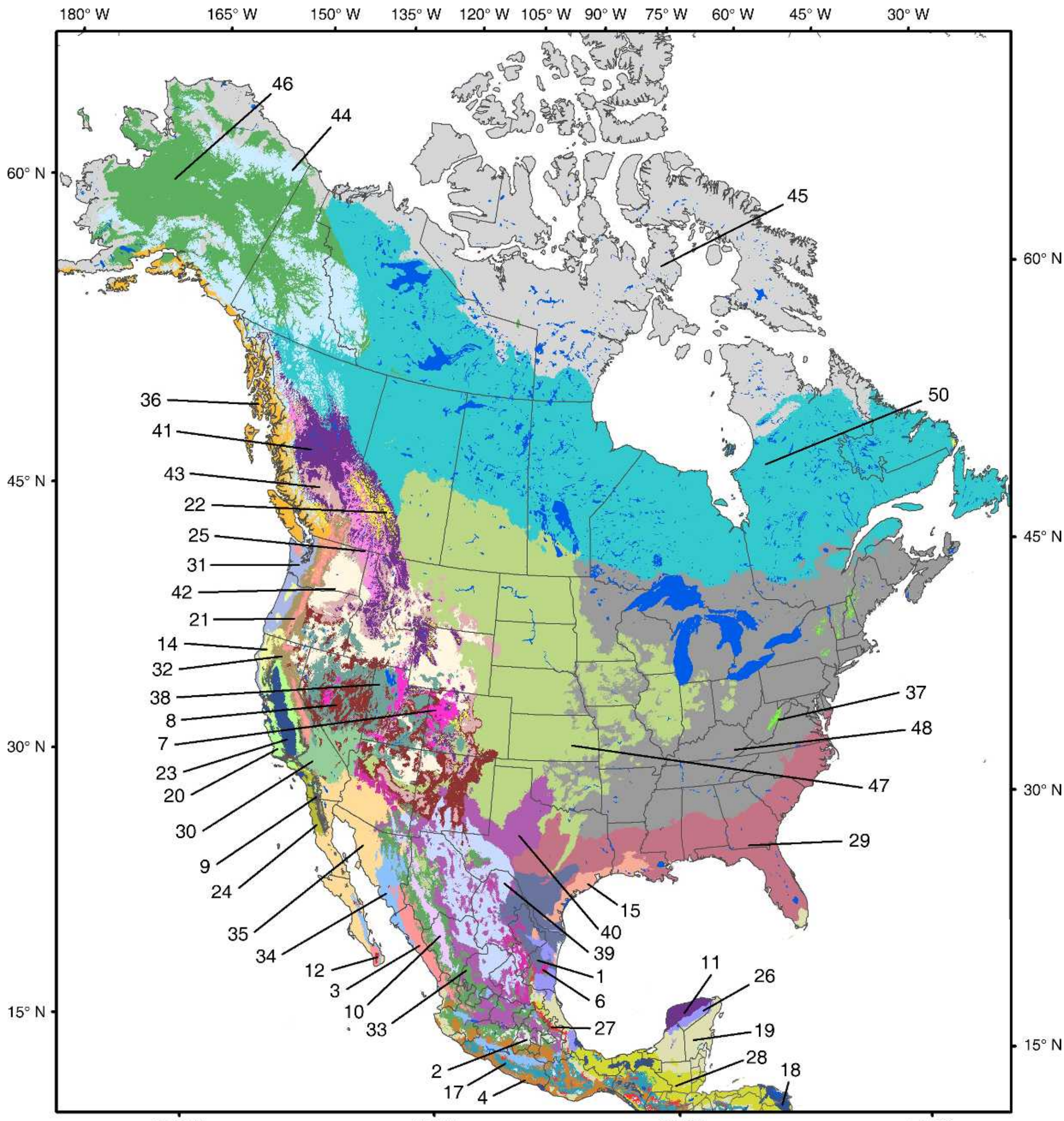

FIG. 1. Predicted contemporary distribution of 46 North American biomes. Biome code numbers are keyed to Table 1.

follow these general trends, but instead are expected to find suitable future climates at the same locations where they are found today, include the dry tropical forests (3 and 11), the desert biomes (35 and 39), the Great Plains (47), forests of eastern USA (29 and 47), and the arctic tundra (45). Alternatively, several biomes must shift in their entirety if they are to inhabit in the future the climates in which they occur today: Rocky Mountain tundra (22) and subalpine forests (41); the conifer forests and cloud forests of Mexico (2, 10, 27); and the subalpine forests and tundra (37) of the East.

Agreement among projections in consensus maps (Fig. 4) can be seen by superimposing projections (Figs. 5 and 6). The 2060 projections tend to agree, for instance, that climates suited to tropical dry deciduous forests (Fig. 5a), montane scrub (Fig. 5b), interior cedar–hemlock forests (Fig. 5c), and coastal hemlock forests (Fig. 5d) should expand, the latter not only northward along the coast but also into the Rocky Mountains of the interior. Agreement is also high for the expansion of desertscrubs (Fig. 6). If one considers only those grid cells of Fig. 6b for which four or more of

TABLE 4. Bioclimate model predictions of contemporary biome area and the consensus impact of six projections on total area, area unaffected, and occurrence of no-analog climates in three time periods.

Biome code	Predicted area (thousands of km^2)	Change in area (% of present)			Remaining unchanged (% of present)†			No contemporary analog (% of future)‡		
		2030	2060	2090	2030	2060	2090	2030	2060	2090
Primarily Mexico										
1	183.8	1	33	64	76	60	34	28	66	66
2	28.9	−68	−84	−92	26	13	7	0	0	0
3	84.4	71	114	184	88	83	79	7	9	20
4	145.0	33	26	28	68	56	52	2	4	15
6	77.6	−47	−58	−76	32	19	10	1	8	7
10	58.5	−37	−67	−85	47	28	14	0	0	0
11	99.0	174	169	293	99	96	99	22	65	77
12	2.1	−65	20	26	12	23	8	1	0	2
17	119.6	−19	−44	−65	48	32	21	0	0	1
18	56.7	26	14	−26	43	27	9	49	79	91
19	354.8	−20	−15	−1	50	50	41	27	38	62
26	64.6	−82	−90	−98	7	2	0	4	5	0
27	30.6	−77	−82	−96	12	4	0	0	0	0
28	205.8	5	12	4	70	74	72	5	14	33
33	265.9	8	10	−8	62	57	47	0	0	0
34	117.9	47	85	176	72	66	66	10	22	31
35	290.3	27	59	105	96	98	98	1	1	3
39	367.3	31	29	−2	84	70	47	0	1	3
40	443.3	−12	−5	−1	51	37	29	2	4	6
Primarily conterminous United States										
7	76.0	59	87	166	59	49	42	1	2	6
8	385.2	−10	−21	−40	49	33	23	0	0	0
9	46.2	−5	−18	−22	41	35	29	4	9	13
14	42.2	−17	2	−22	49	47	30	2	5	15
15	74.3	−25	−9	−12	49	57	37	30	57	99
20	60.5	25	51	57	61	62	57	10	23	21
21	78.0	−48	−70	−73	41	27	17	0	0	6
23	67.3	−24	−47	−73	61	40	18	20	37	31
24	23.5	6	48	24	56	52	24	23	34	37
25	115.8	98	119	134	88	65	57	4	5	0
29	771.9	−6	2	16	83	82	75	7	28	68
30	125.9	5	40	47	77	65	64	1	3	7
31	91.1	8	19	−32	88	76	43	1	12	24
32	127.0	−9	−5	31	59	51	56	1	4	6
37	17.8	−38	20	−61	13	5	0	0	1	4
38	301.4	56	45	105	75	67	78	1	2	2
42	518.9	−27	−33	−41	46	35	28	0	4	9
43	323.0	−2	48	24	51	41	25	0	3	9
47	2457.7	5	15	14	75	72	70	0	1	1
48	2928.7	38	49	68	96	91	90	0	1	1
Primarily Canada and Alaska										
22	77.5	−84	−98	−99	14	1	0	0	4	10
36	260.3	47	88	68	92	86	84	1	3	6
41	431.7	6	−24	−19	53	19	12	0	4	6
44	744.7	−40	−61	−74	52	33	18	0	0	1
45	2942.3	−9	−20	−32	87	77	65	0	0	0
46	971.4	22	51	56	45	38	26	0	1	1
50	4624.4	−14	−23	−22	67	52	49	0	0	1

Notes: Projected areas of distribution are from the consensus of six projections (Fig. 4) from three General Circulation Models (GCM) and two greenhouse gas emissions scenarios. Numeric codes for biomes are keyed to Table 1.

† Percentage of the contemporary area predicted to be suited to the biome existing there today.

‡ Percentage of future area expected to have climates with no contemporary analogs among the biomes of today.

the projections are in agreement, climates suited to desertscrubs should increase by ~25% (333 500 km^2) by 2060. The northern limit of climates suitable for biome 24 is projected to move northward along the California coast by about 550 km; that for biome 38 by 775 km; and that for biome 30 by nearly 1000 km. Although disagreement among the projections tends to be widespread, a large portion of the uncertainty in Fig. 6b results from a failure among the projections to agree on which desertscrub the future climate should suit; that is, biome 30 vs. 38, or 35 vs. 39.

To aid decision-making in the face of large but uncertain changes, we prepared an overlay for the consensus map (Fig. 4) on which were marked grid cells

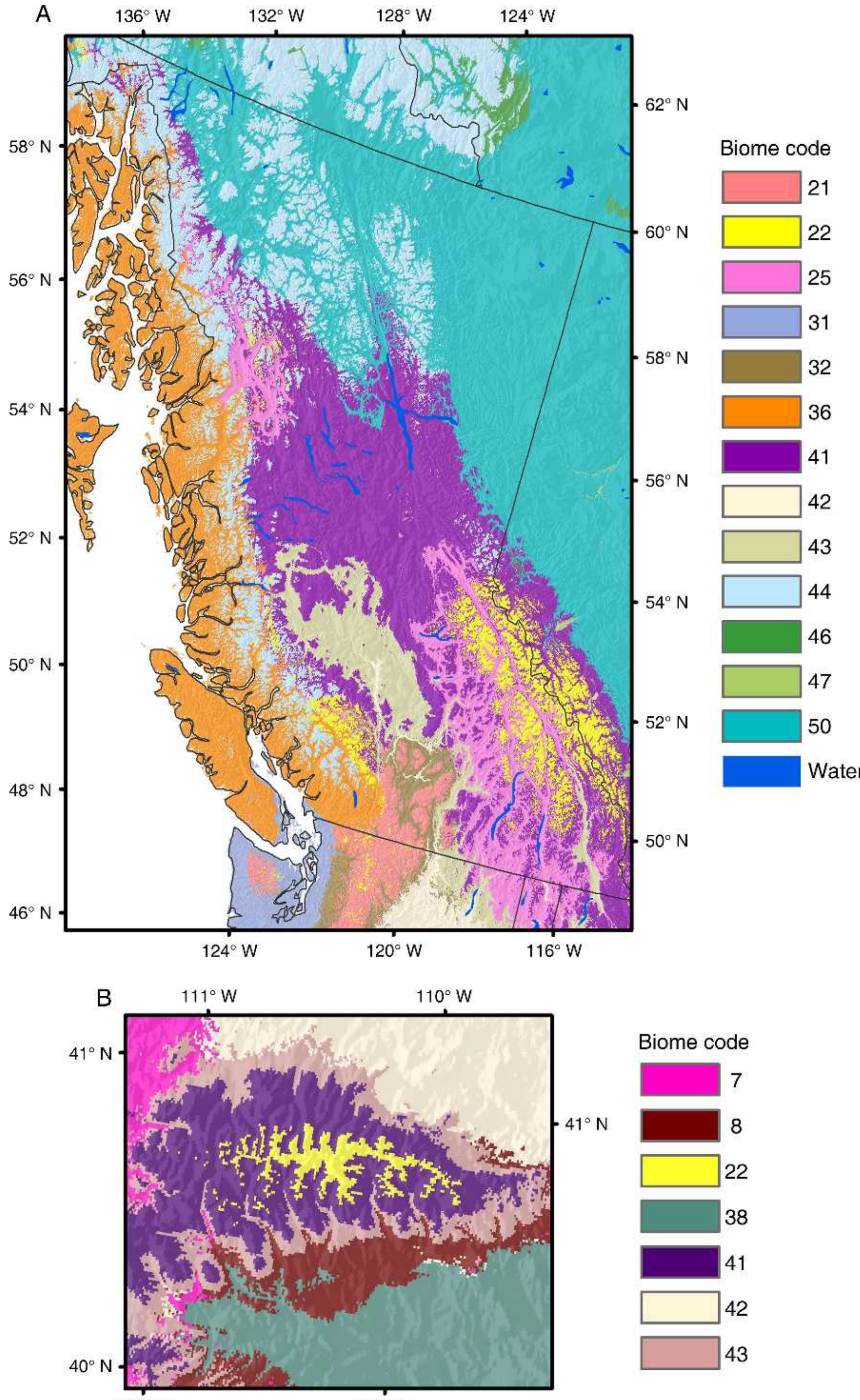

FIG. 2. Predicted distribution of biomes (A) across the geographic and altitudinal vegetation transitions of British Columbia, Canada and (B) for the altitudinal gradients in the Uinta Mountains of northern Utah, USA. Biome codes of color chips are keyed to Table 1.

for which projections were particularly equivocal; that is, agreement of three or fewer projections is viewed as uncertain, while that of four or more is considered to be of greater likelihood. Using these limits assures that a robust prediction will encompass projections from both scenarios (see Appendix C for a discussion of agreement among projections). Fig. 7a, for instance, indicates a loss of climates suited to eastern subalpine vegetation (37) is

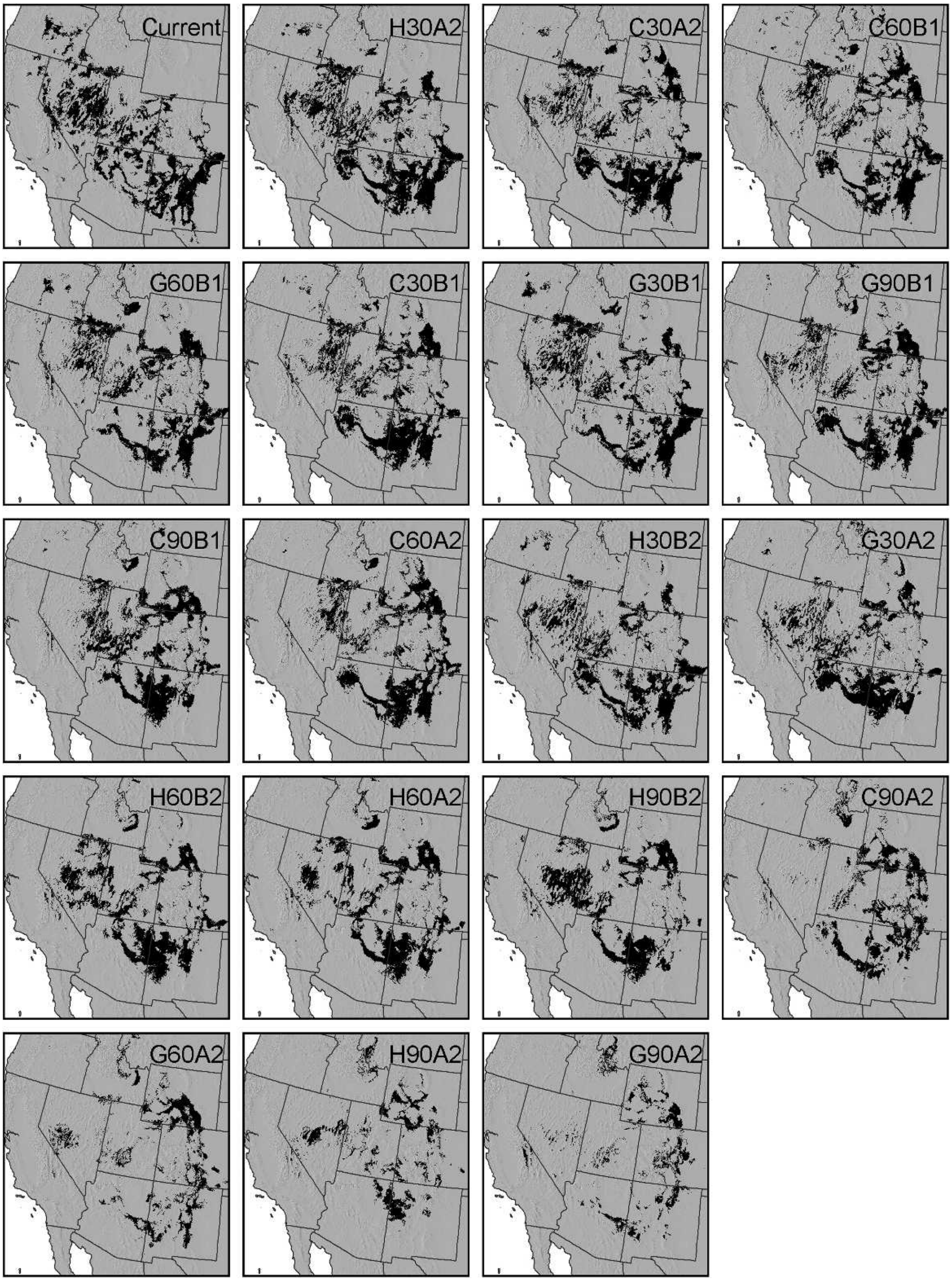

FIG. 3. Predicted climatic niche of Great Basin Conifer Woodland (biome 8) for the current climate (upper left) and for climates of three General Circulation Models (GCMs) and two greenhouse gas emissions scenarios for three time periods arranged (left to right, top to bottom) according to declining projected area. Abbreviations are: (for the GCM): C, Canadian; G, Geophysical Fluid Dynamics Laboratory; H, Hadley Centre; (for the year) 30, 2030; 60, 2060; 90, 2090; (for the scenario) A2, high greenhouse gas emissions; and B1 and B2, low emissions.

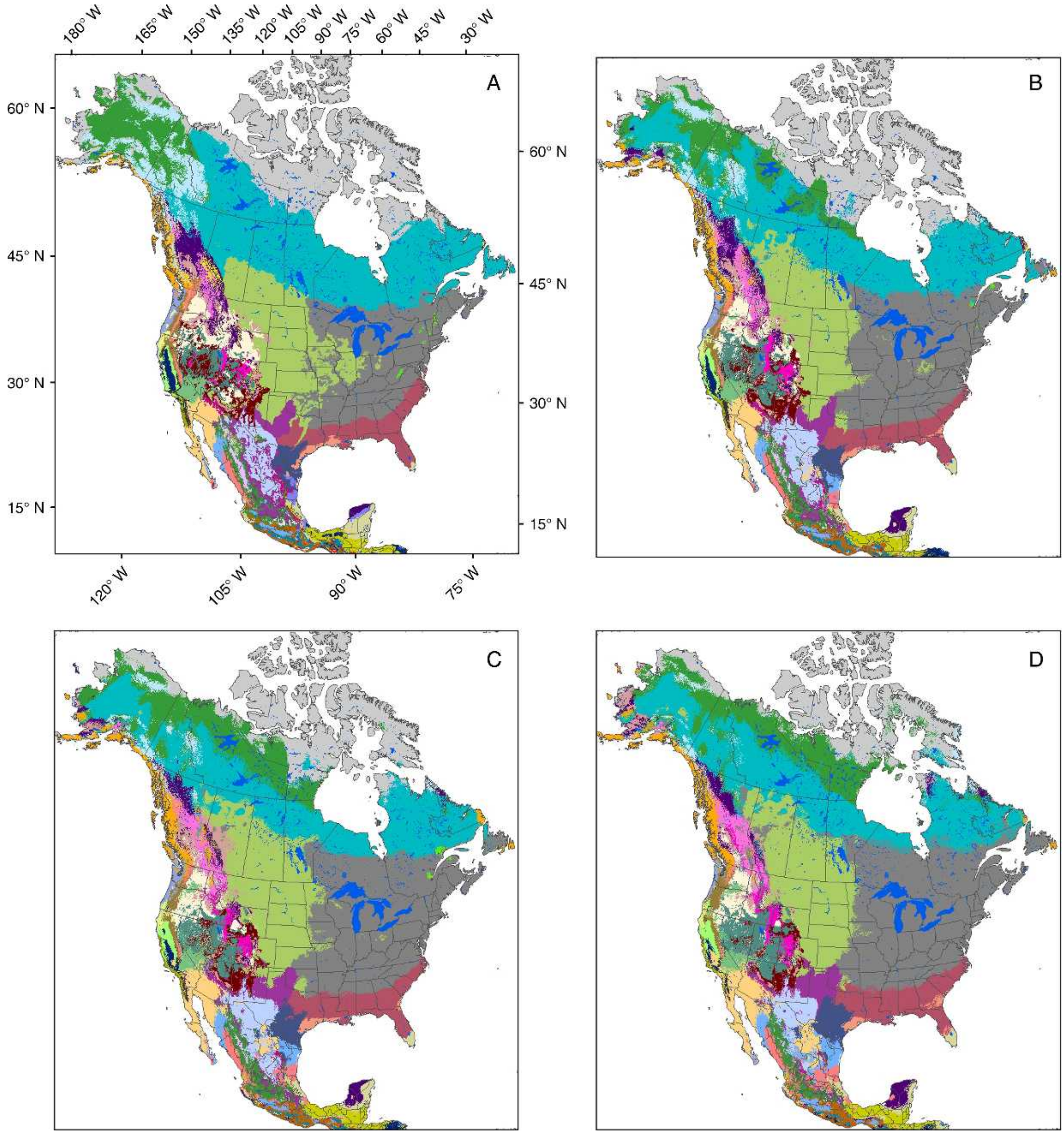

FIG. 4. Predicted distribution of biomes for (A) the contemporary climate and the consensus maps for the decade surrounding (B) 2030, (C) 2060, and (D) 2090 (i.e., 2026–2035 for 2030). Consensus is determined by the plurality of six predictions: two greenhouse gas emission scenarios for each of three general circulation models. Biome color codes are keyed to Fig. 1.

likely by 2060, but that the ecotone between the temperate deciduous forests (48) and evergreen–deciduous forests (29) should remain stable. Uncertainty tends to be centered on whether climate suitable for the eastern outliers of the Great Plains (47) would remain. Fig. 7b likewise shows that a 400 km northward expansion of the climate suited to the temperate deciduous forests (48) into that currently inhabited by the Canadian Taiga (50) is to be expected, while confusion tends to be centered on the location of boundaries between biomes. By contrast, Fig. 7c shows an area in southwestern USA for which uncertainty is rampant. While the projections agree that the lower elevations should be suitable for desertscrubs, the location of boundary between the Sonoran (35) and Mojave (30) deserts is problematic. Whether the climate of the surrounding mountains would be suited for grassland, woodland, or forest is also equivocal.

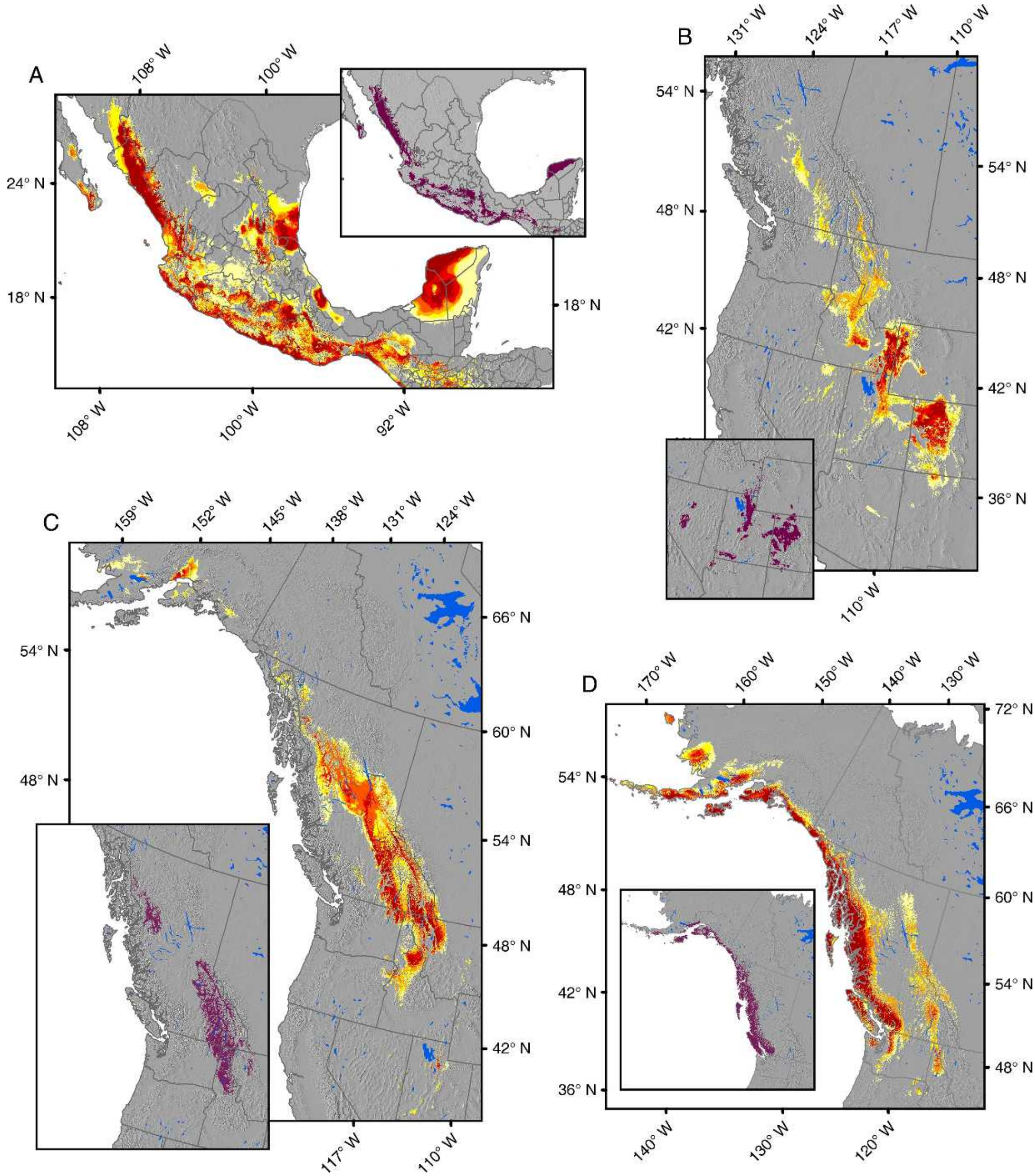

FIG. 5. Predicted contemporary distribution (insets, maroon) and mapped projections for the decade surrounding 2060 superimposed for three GCMs and two greenhouse gas emissions scenarios for (A) Tropical Dry Deciduous Forests, (B) Great Basin Montane Scrub, (C) Interior Cedar–Hemlock Forest, and (D) Coastal Hemlock Forest. Shading indicates the number of projections that agree: light yellow, 1 projection; dark red, 6 projections.

Climates without contemporary analogs

Uncertainty is reflected not only by disagreement among projections, but also by the dispersion of future climates having no contemporary analogs to those of the North American biomes. The maps in Fig. 8 convey a high likelihood that no-analog climates should arise early and increase in concentration throughout the century particularly along the Gulf of Mexico, but also in the interior Northwest of the United States and adjacent Canada, through much of California on the west coast, and sporadically through the arctic.

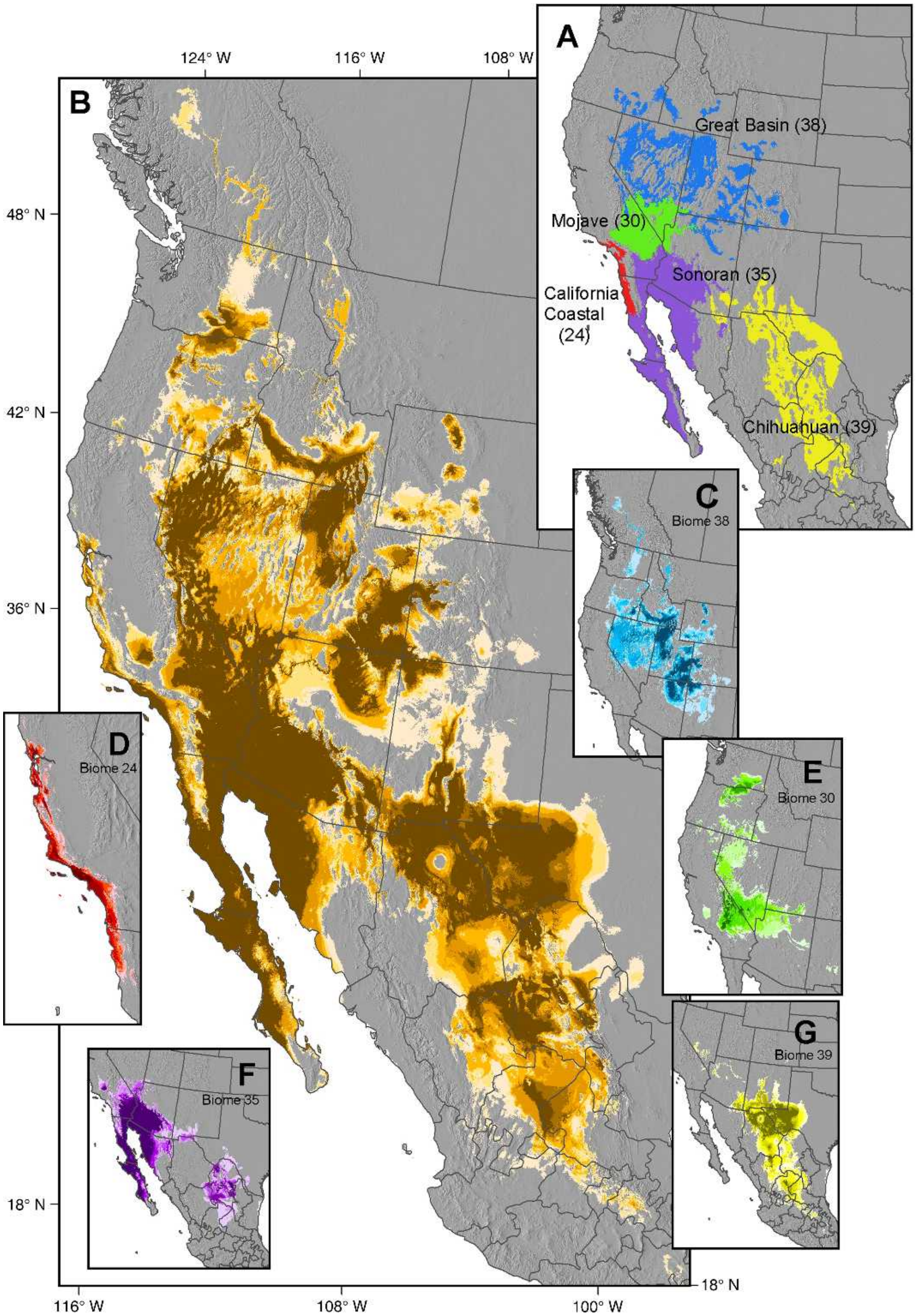

FIG. 6. (A) Predicted distributions of five desertscrub biomes of western North America, (B) projections for desertscrubs in total for the decade surrounding 2060, and (C–G) projections for the five individual biomes for the decade surrounding 2060. In all panels except A, projections from three GCMs are superimposed, with shades of color coding concurrence: lightest, 1 projection; darkest, 6 projections. Color paths of panels C–G are linked to panel A, and numbers in parentheses in panel A are biome codes, which are keyed to Table 1.

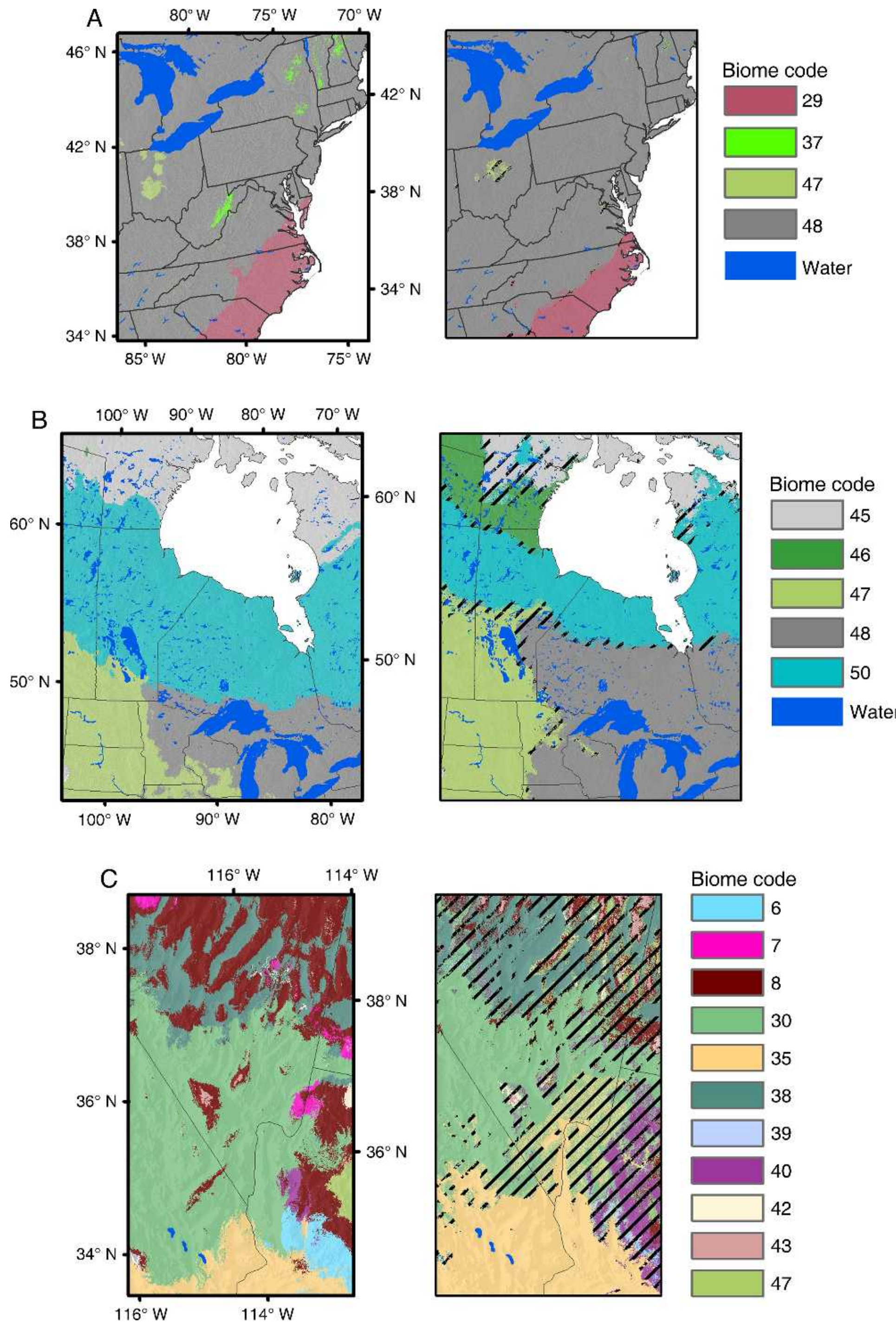

FIG. 7. Three sets of panels comparing contemporary distribution of suitable climates (left) with the consensus of six projections for the decade surrounding 2060 (right) for (A) eastern USA, (B) Ontario and Manitoba, Canada, and (C) southern Nevada, USA. Hatch marks indicate grid cells for which three or fewer of six projections were in agreement. Biome codes of color chips are keyed to Table 1.

Especially pertinent are predictions in Fig. 8a of few North American analogs in the Caribbean Islands. Because Brown's (1994) classification included unique biomes for the Caribbean that we ignored, all climates of the Caribbean are for biomes outside the climatic range of the 46 biomes used in our model, that is, they should lack analogs. Of the 267 300 terrestrial grid cells in the Caribbean, the climate in 81% was predicted to be suited

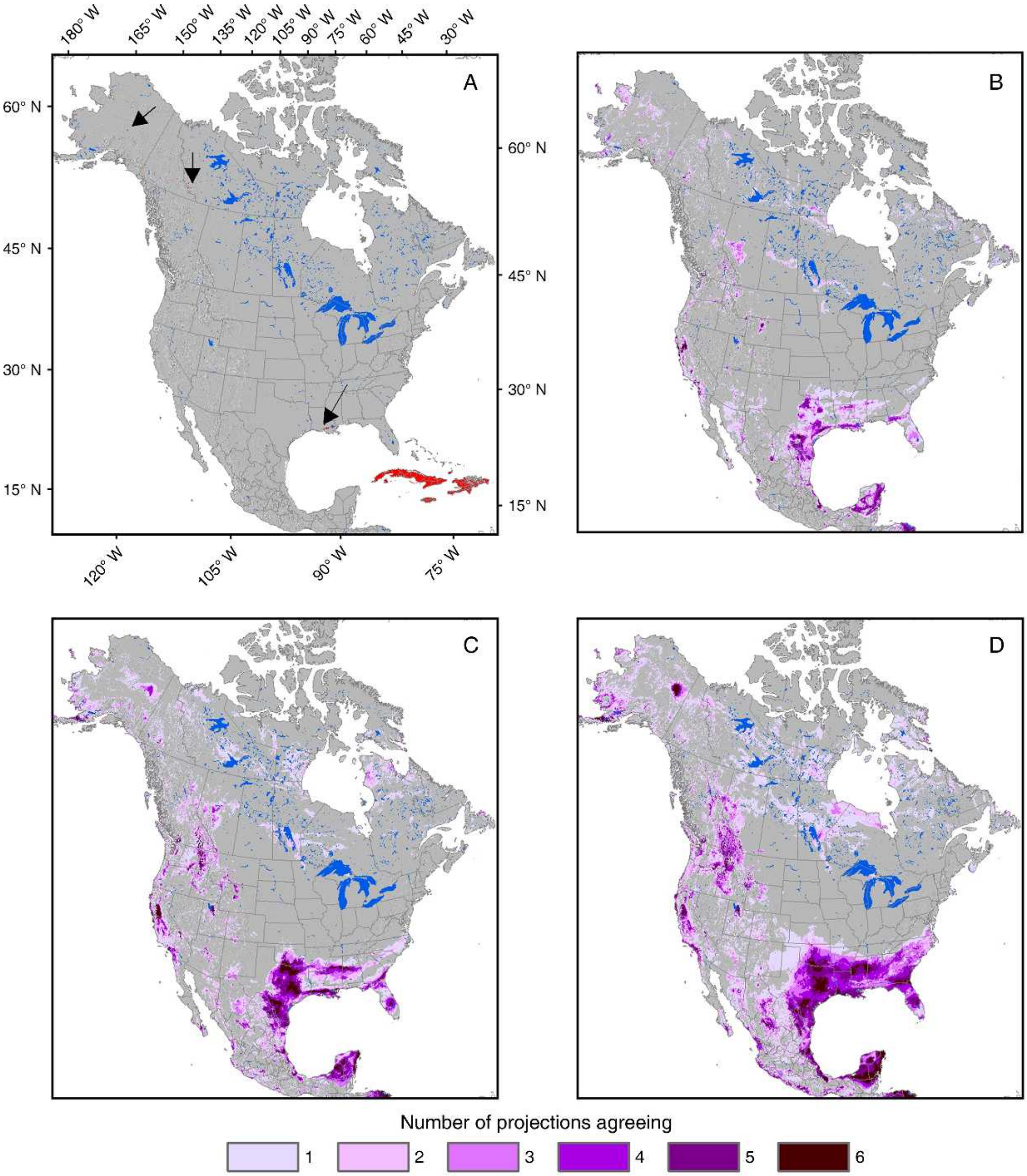

FIG. 8. Mapped predictions of climates without contemporary analogs among 46 North American biomes for the (A) contemporary climate and for climates for the decade surrounding (B) 2030, (C) 2060, and (D) 2090. In panel A, grid cells with climates lacking analogs are colored red; arrows point out several areas in red that are difficult to see. In panels B–D, six projections are superimposed, and grid cells having climates without contemporary analogs are colored according to the agreement among six projections.

to biome 99, that is, no-analog climates. Climates of the remaining grid cells were analogous to either the tropical semi-evergreen forests (19) or tropical dry deciduous forests (4 and 11). These results, therefore, provide additional verification of our procedures for identifying no-analog climates.

The isolated specks of no-analog climates predicted for the current climate (Fig. 8a) along the Gulf Coast of

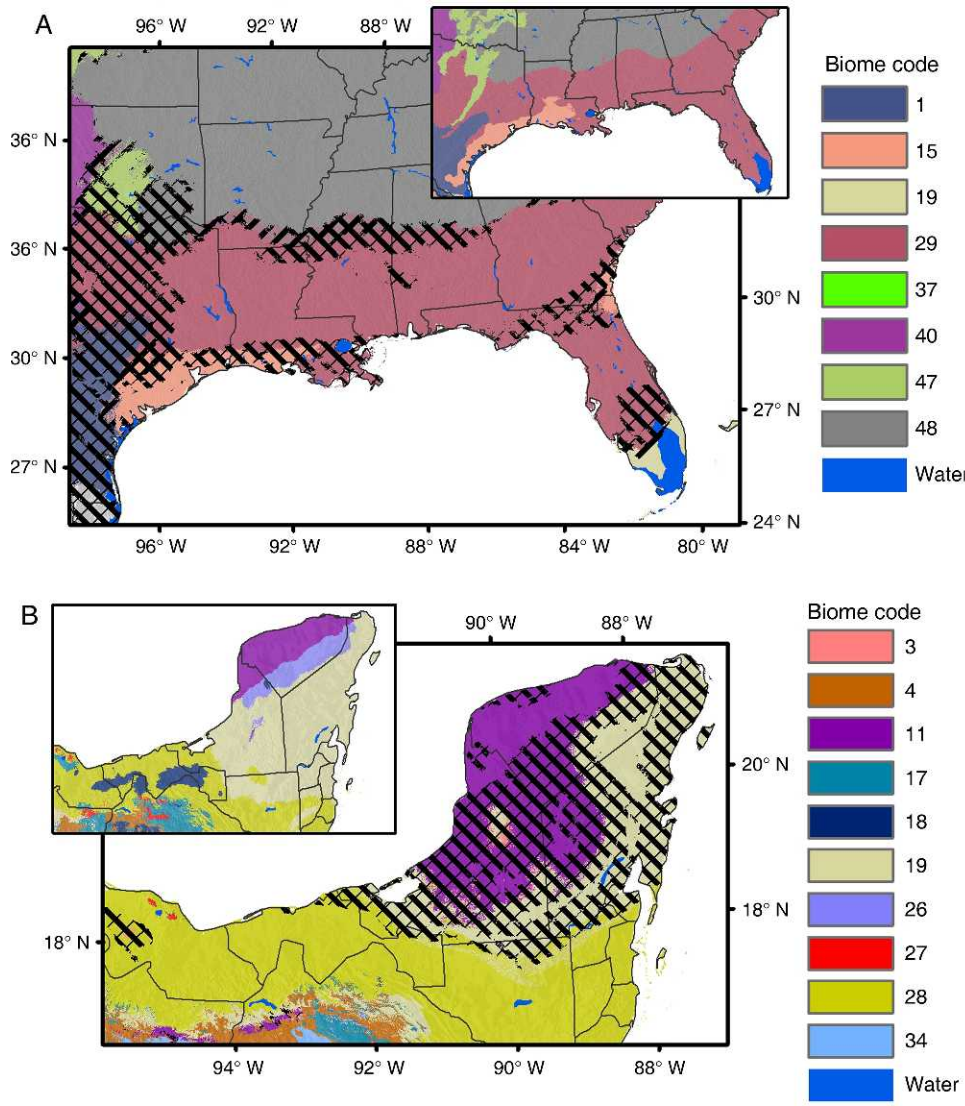

FIG. 9. Contemporary (insets) and future (decades surrounding 2060) consensus projections for (A) the Gulf Coast of southeastern USA and (B) the Yucatan Peninsula of Mexico. Grid cells projected to have no contemporary climatic analog by at least four of six projections are marked with crosshatching. Biome codes of color chips are keyed to Table 1.

United States and in the Arctic communities of the far northwest undoubtedly reflect errors of prediction most likely arising from either the climate surfaces or the Random Forests model. Their paucity, however, reflects the good fit of the statistical model.

Applications in land-use management

To illustrate applications in land-use planning, we chose examples of different resolution and complexity (Figs. 9–11). Fig. 9 deals with uncertainty imposed by novel climates; Fig. 10 with uncertainty due to disagreement among projections; and Fig. 11 with six high-resolution examples where either or both sources of uncertainty may infringe on land-use decisions. Maps such as these would allow managers to take into account the consensus from disparate projections, confidence in the predictions, and likelihood that the future climate will be without contemporary analogs.

DISCUSSION

Our analyses have shown that (1) the Random Forests classification tree can accurately predict the current distribution of North American biomes from climate variables (see also Rehfeldt et al. 2006, Iverson et al. 2008), (2) large-scale classification problems can be accommodated by the statistical procedures, and (3) climates beyond the limits of the contemporary biomes can be identified.

From a statistical viewpoint, only 3.7% of 1.75 million observations were misclassified by our model. In

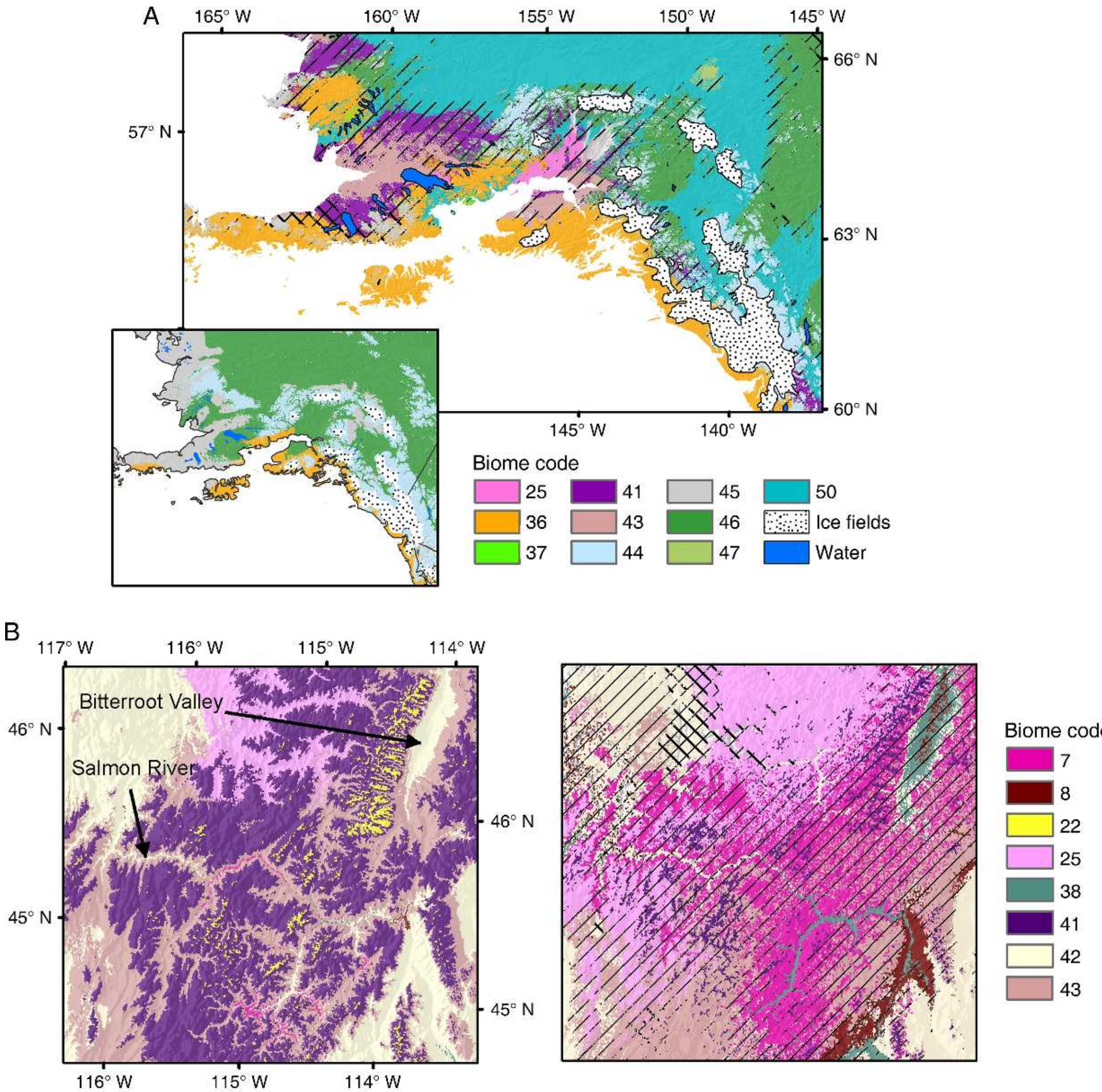

FIG. 10. Prediction of suitable climates for biomes in the contemporary climate (inset in panel A, left-hand panel in panel B) compared to those for the decade surrounding 2060 for (A) the south shore of Alaska, USA, and (B) the Salmon River Drainage of the interior West, USA. Crosshatching indicates grid cells expected by four or more of the six projections to have 2060 climates with no contemporary analog; hatching indicates grid cells for which three or fewer of six projections were in agreement. Numeric codes of color chips are keyed to Table 1.

calculating errors of prediction, however, one assumes that the classification of an observation was without error. In our analysis, most of the classification error involved biomes occurring in altitudinal sequences, a result undoubtedly due to broad ecotones that would make classification tenuous. Using a statistical algorithm with the power of Random Forests thus meant that the accuracy of the predictions was more dependent on the quality of the input data rather than errors of fit. Besides using supplemental information to better define biomes shown previously to be easily confused, we also incorporated a robustness to our analysis by demanding that two-thirds of the "forests" contain classes that should be most difficult to separate. For a broad, heterogeneous region such as North America, it is difficult to envision vegetation models with greater statistical precision. This precision attests to the strong climate controls of biome distribution.

Our analytical approach of assembling the data into numerous "forests" each containing a subset of the

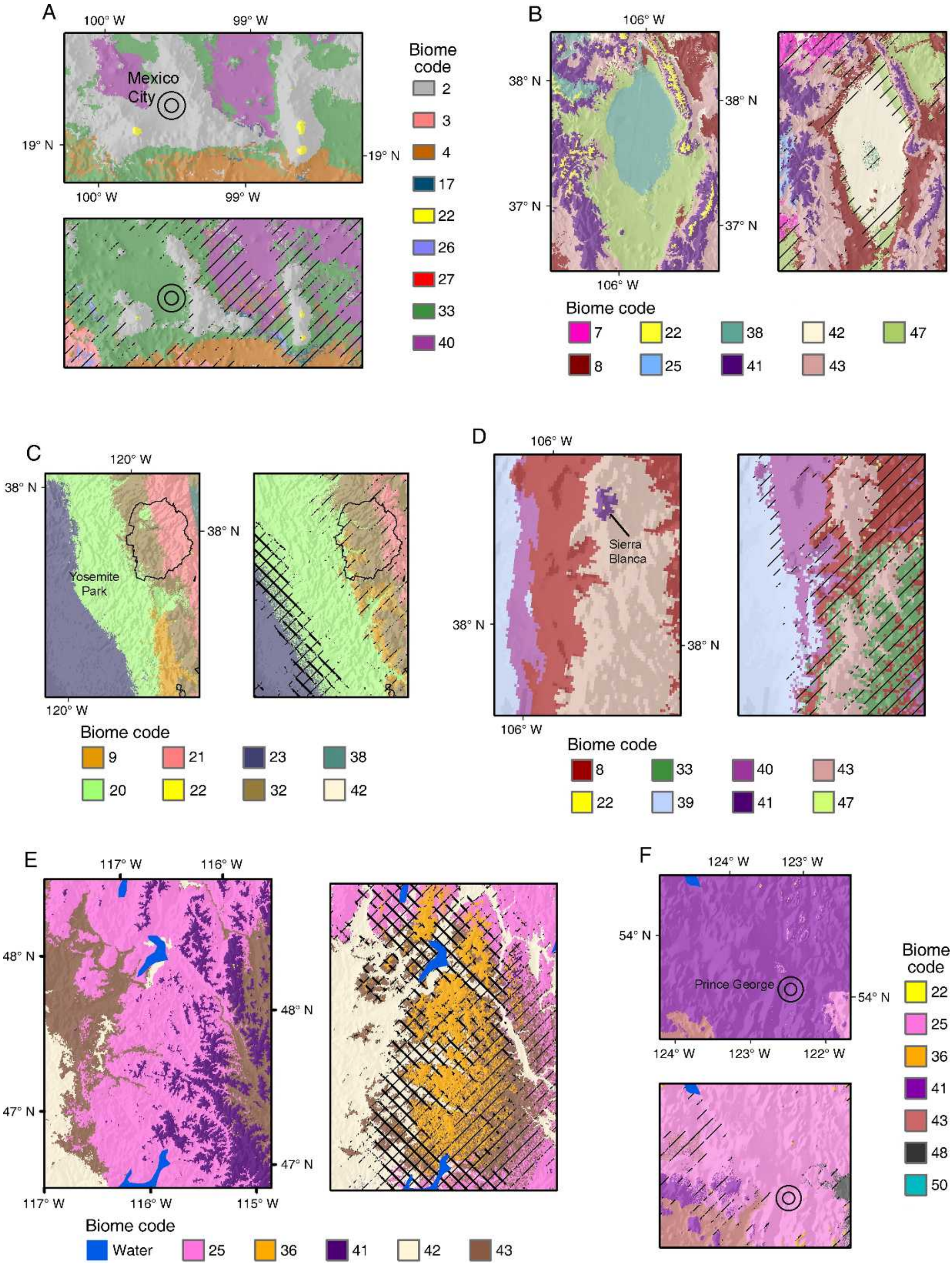

FIG. 11. Prediction of suitable climates for biomes in the contemporary climates (top in panels A and F; elsewhere, left-hand panel) compared to those predicted for the decade surrounding 2060 (bottom in panels A and F; elsewhere, right-hand panel) for (A) the Transvolcanic Axis of Mexico; (B) the San Luis Valley in Colorado, USA; (C) Yosemite National Park in California, USA; (D) the Sacramento Mountains in southern New Mexico, USA; (E) northern Idaho of the interior Northwest, USA; and (F) the

biomes circumvented the limit to the number of classes that can be used in the Random Forests algorithm. Our model uses 46 classes instead of the ceiling of 32 specified by the algorithm, but the implication is that many more classes could be handled in a similar manner.

Identifying climates without contemporary analogs

Heretofore, identification of novel climates in vegetation modeling has relied on climate thresholds, above or below which one assumed that the climates were no-analog (e.g., Hansen et al. 2001, Rehfeldt et al. 2006). Our approach was to establish a fictitious class in each "forest" that contained observations outside the range of climates characterizing the biomes in the "forest" yet within the range of climatic conditions known to occur throughout North America. For prediction, this fictitious class provided the algorithm an opportunity to reject all actual biomes.

Two empirical tests strongly support the validity of our methods. About 78% of the world climates tested and 81% of data points from the Caribbean Islands were classified as having no analogs to those of North American biomes. Of those data points classified as having analogs (Table 3), most predictions were intuitively reasonable. One could expect, for instance, tropical semi-evergreen forests (19) of Mexico to have analogs in the Caribbean and for the Great Plains Grassland (47) to have analogs in Asia.

Perhaps more pertinent is the agreement between our projections and the novel climates mapped globally by Williams et al. (2007) using GCM climate output directly. Both analyses pinpoint the Gulf Coasts of Mexico and the United States as being particularly ripe for the future occurrence of novel climates.

Concurrence with regional models

Our projections for the coming century (Fig. 4) describe (1) an explosion of climates suited to tropical dry deciduous forests, (2) increased aridity leading toward additional desertification of northern Mexico and western USA, (3) widespread loss of alpine tundra climates, (4) northward expansion of climates typical of prairies and temperate deciduous forests, (5) stability of climate boundaries of the evergreen–deciduous forests of southeast USA, and (6) compression of climates suited to taiga and tundra of the far north.

In comparison to regional models, our results are essentially the same for western USA as those of Rehfeldt et al. (2006), who used an approach that was much similar; strongly support the empirically based statistical models of Iverson et al. (2008) for the eastern USA, particularly in describing a stable boundary between temperate forests and deciduous–evergreen forests; and are surprisingly consistent with those of Hamann and Wang (2007), who used different methods, GCMs, and emissions scenarios to produce a model for British Columbia, Canada. In regard to the latter model, a minor point of contention arises toward the end of the century in the northeast portion of the province, where their model predicts climate suited to a montane forest, while ours predicts climate suited to the Great Plains (47). Because they worked with current ecosystems of only British Columbia, these grassland ecosystems were not an option for their future projections, that is, their model did not allow for the expansion of vegetation from other parts of North America into British Columbia. Otherwise, this regional model and its latest iteration (E. Campbell, *personal communication*) closely parallel our results by suggesting, in particular, the proliferation of climates typifying the interior cedar–hemlock biome (25) and the future occurrence of climates typical of coastal hemlock forests in the Rocky Mountains (36).

Output from another empirical model for Alberta, Canada (Schneider et al. 2009), is difficult to compare with Fig. 4 largely because of disparate classification systems. Nonetheless, the Alberta model, like ours, depicts the northward expansion of grassland climates at the expense of those of the taiga. Our results also complement regional models in Mexico (Gómez-Mendoza and Arriaga 2007, Zacarías-Eslava and Castillo 2010) purporting an altitudinal upward shift of climates suitable to chaparral and pine–oak woodlands that eventually would supplant habitats currently suited to coniferous forests.

Our results, however, conflict with those using a mechanistic model for the United States (Bachelet et al. 2001, 2008, Hansen et al. 2001) that purport a proliferation of woodlands in the East and interior West, expansions of grasslands in the Midwest, and a notable lack of desertification for much of the West. Yet, this same mechanistic model produces essentially the same projections as ours for Alaska (Fig. 10a; Bachelet et al. 2005) along with equivocal results for California, USA (Lenihan et al. 2003). In the latter instance, the mechanistic model projects an increase in climates suited to woodlands in northern California, which we corroborate (Fig. 4), but for southern California, it projects increases in climates suited to grass and shrub communities, while we project increased desertification.

The proliferation of arid climates suited to desert-scrubs, thornforests, and tropical dry forests that we project parallel estimated increases in drought frequen-

←
upper Frasier River near Prince George, British Columbia, Canada. Crosshatching marks grid cells expected by four or more of the projections to have 2060 climates with no contemporary analog; hatching marks grid cells for which three or fewer of six projections were in agreement. Biome codes of color chips are keyed to Table 1.

cies in western USA and Mexico, which could extend into Canada if emissions continue unabated (Sheffield and Wood 2008). A broad consensus of climate modelers support this increase in aridity for western North America (Seager et al. 2007), as do the increases in temperature in northwestern and central Mexico that already have occurred (Pavia et al. 2009).

Land-use management

To make informed decisions, land managers must assimilate forecasts about the future distribution of climatic niches with measures of uncertainty that may stem either from variation among disparate projections or from the likelihood that future climates may be novel. Our assumption is that resources are best invested where the best-suited vegetation for future climates can be predicted with a high degree of certainty, that is, where there is an absence of novel climates and where projections are in agreement. Management strategies for dealing with high uncertainty must invoke risk assessments that not only address potential trade-offs among negative management outcomes, but also incorporate a degree of flexibility in management frameworks that can accommodate this uncertainty.

In some regions, management alternatives seem straightforward. In southeastern Canada (Fig. 7b), for instance, projections from disparate GCMs and emissions scenarios tend to agree, and future climates are expected to be analogous to the contemporary. Managers, therefore, can anticipate the changing climate to become more suited to species typical of temperate deciduous forests (48) than those of the contemporary taiga (50).

In other regions, strategies for land use become more complex. Management alternatives for climates without contemporary analogs are largely unexplored, yet novel climates should dominate much of the landscape surrounding the Gulf of Mexico (Figs. 8 and 9). Natural resource managers in southeast USA may be dealing, on the one hand, with prairies or savannas encroaching on evergreen–deciduous forests or, on the other, the conversion of contemporary forests to highly productive foreign species such as *Pinus patula* of Mexico. Managers in the Yucatan of Mexico could be contending with the encroachment of tropical climates that are more arid than those of today. The impact of these novel climates on Yucatan agriculture, particularly corn production, is largely unexplored.

Despite disagreement among projections and an expectation for patches of novel climates along Alaska's (USA) south shore (Fig. 10a), future climates presage an influx of Rocky Mountain conifers (41 and 43) and Canadian Taiga (50) at the expense of the alpine tundra and subarctic conifers that occur there today. Although a warming climate undoubtedly will also affect the ice fields of Fig. 10, our models are not capable of addressing rates of glacier retreat.

Future climates projected for much of the Salmon River Drainage and Bitterroot Valley (Fig. 10b) of the U.S. interior Northwest, however, are so uncertain that land-use planning becomes highly problematic. Even so, the likelihood is high that patches of climates suitable for interior cedar–hemlock forests (25) should develop in the north, for montane forests (43) in the south, and for montane scrub (8) in some valleys, particularly the Middle Fork of the Salmon River.

Fig. 11 presents high-resolution projections for six land-use case studies. In the Transvolcanic Axis of Mexico (Fig. 11a), forest managers likely will be contending with the upward expansion of arid climates (Figs. 5a, 6f, and 6g) that would infringe on the pine–oak woodlands (33 and 17) and, in turn, supplant conifer forests (2). Although uncertainty on the 2060 Transvolcanic landscape is high, much of it deals with ecotones between pine–oak forests and grasslands; that is, conflicts between timber management, corn and wheat production, and grazing. Conifer forests undoubtedly will be migrating onto the flanks of the several volcanoes where Ledig et al. (2010) already have suggested establishment of reserves for *Picea* spp.

In the San Luis Valley in southern Colorado, USA (Fig. 11b), much of the uncertainty facing land managers would concern which grassland (biome 42 or 47) should dominate the valley floor. While the distinction between these grasslands may be inconsequential to land-use decisions, agreement among projections for the surrounding mountains would purport the conversion of much of the subalpine forests (41) to montane forests (43). Somewhat perplexing is the likelihood that a portion of the 2060 landscape should be climatically suited to the interior cedar–hemlock forests (25) that currently occur 1300 km to the northwest. Seemingly anomalous predictions such as these underscore the enormity of the potential impact of climate change on the vegetation. This counterintuitive projection, for instance, may simply be suggesting a higher productivity of the future forests than of the montane forests that occur there today, but future forests still could be suited to montane forest species, some of which (e.g., *Pinus ponderosa*, *Pseutodsuga menziesii*) occur in both biomes 25 and 43 today.

In California, USA, novel climates are projected for the interface between valley grasslands (23) and woodlands (20), while disagreement among projections tends to center on the mountain ecotones (Fig. 11c). Nonetheless, it is likely that climates of contemporary biomes will be pushed upwards along the west slopes of the Sierra Nevada, demanding, for instance, that managers of Yosemite National Park deal primarily with montane (32), or even chaparral (9) species, rather than those of the subalpine (21) forests.

In the Sacramento Mountains of southwestern USA (Fig. 11d), the current vegetation is arranged on an altitudinal sequence from desert (39), semi-desert grassland (40), woodlands (8), montane conifer forest

(43), subalpine forest (41), and alpine tundra (22) at the top of Sierra Blanca. While the climate of 2060 should eventually shift these biomes upwards to the extent that climates suitable to tundra and subalpine vegetation are largely lost, a lack of agreement among the projections makes questionable whether the mid-elevation climates would be suited to Rocky Mountain conifers (43) or to the pines and oaks of the Madrean woodlands (33).

Northern Idaho, USA (Fig. 11e) may be well situated for documenting the impacts of a changing climate as they unfold. Current altitudinal distributions include grasslands (42) at the lowest elevations, a sequence of coniferous forests (43, 25, and 41) at the middle elevations, and alpine tundra (22) at the highest. Projections agree that climates suited to grasslands should expand, while those suited to subalpine and tundra biomes should rapidly disappear. Projections also tend to agree that (1) mid- to high elevations should be suitable for species of the Coastal Western Hemlock biome (31) that occurs today 600 km to the west, but (2) climates without contemporary analogs should insinuate themselves between those of the grasslands and hemlock forests. This belt of novel climates might be suited to a mixture of coastal and inland species that do not associate today.

Fig. 11f suggests that land managers near Prince George, British Columbia, Canada, probably will be contending with a conversion of subalpine forests (41) to cedar–hemlock forests (25). Of particular interest, however, is a parcel of land east of Prince George projected to have a climate suited to the temperate deciduous forests (48), which currently occur 2000 km to the east (Fig. 1). This prediction, along with those for climates suited to biome 48 occurring in the prairie provinces of Canada (Fig. 4), may represent a correction of the Brown et al. (1998) biome classification, which omits aspen parklands (see Schneider et al. 2009). Aspen (*Populus tremuloides*) occurs in the northern extent of temperate deciduous forests (see Iverson et al. 2008), but data points from the parklands were treated by us as Canadian Taiga (50).

Applications and limitations

Our results, like those of many others, show how projected impacts depend on the GCMs and scenarios used for the analysis. One can only speculate on how our results might change when using a different assortment of GCMs and scenarios. Yet, perhaps fortuitously, the six projections we used encompass an extremely broad range of impacts. Our results, moreover, are compatible with those of other correlative modelers who have conducted regional analyses with disparate GCM formulations and disparate methods. By focusing interpretations on the similarities among a broad range of projected responses, robust recommendations apparently can be produced despite the nuances of individual GCMs.

This analysis of potential responses of North American biomes to climate was stimulated by the need for land management guidelines during climate change. We present statistically robust models that can be used at resolutions suitable for decision-making on local landscapes. Limitations of our work relate mostly to the accuracy by which the original classification was mapped and digitized. In addition, our model does not consider edaphic effects, and, therefore, swamps and riparian zones have been ignored. Indeed, the vast Mississippi River bottomlands that were mapped by Brown et al. (1998) have been treated by us as upland forest. We emphasize, moreover, that our model predicts and projects suitable habitat which may or may not reflect actual plant distributions.

For the models to be suited for local interpretation, mapping must be at a relatively fine scale. The maps we present are at 0.0083° grid, which, at the equator, is a 1-km grid. While the continuous climate surfaces we used are capable of mapping at resolutions however fine, climate models are not yet capable of estimating microtopographic effects, particularly those associated with aspect or cold-air drainages. In addition, new procedures (e.g., Hewitson and Crane 2006) for downscaling coarse GCM grids may further improve fine-scale projections, but are not yet readily available. Consequently, effective use of our projections will require implementation by personnel familiar with local landscapes.

Paleocologists have shown convincingly that species response to climate is individualistic (see Jackson and Overpeck 2000, Ackerly 2003, Jackson et al. 2009); species, not associations, respond to climate. Projections for eastern USA (Fig. 7a, Table 4), for instance, suggest that the climate suited to the southern limits of the temperate deciduous forests should remain relatively stable. Yet, within these biomes, one can expect the climate niche of individual species to shift (see Iverson et al. 2008). In addition, broadly dispersed species tend to be composed of populations that are genetically attuned to different portions of the climate gradient occupied by the species as a whole (e.g., Rehfeldt et al. 1999). This means that even in regions such as eastern North America, where biomes may remain static, species assemblages are likely to be in considerable flux as an attempt is made to restore a semblance of equilibrium between climate and plant distributions.

We demonstrate the potential usefulness of biome models in land-use planning during climate change. In most of our examples, the climate surrounding 2060 is targeted for illustration of potential impacts and responses. Practical programs, however, must balance short-term impacts against long-term effects; populations and species poorly adapted in the near future will not achieve the long-term goals. While biome models such as ours can provide tools suited for planning, landscape prescriptions also will require models for the component species (see Rehfeldt et al. 2006, Iverson et al. 2008).

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Supplemental Material

Appendix A

Acquisition of data points used in fitting a Random Forests classification tree to point locations within 46 North American biomes (*Ecological Archives* A022-007-A1).

Appendix B

Projected impacts at the trailing edge summarized for three General Circulation Models and two emissions scenarios (*Ecological Archives* A022-007-A2).

Appendix C

Discussion of agreement and uncertainty among disparate projections (*Ecological Archives* A022-007-A3).