Global Warming and the Species Richness of Bats in Texas

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Abstract: *General circulation models provide predictions for global climate under scenarios of increased atmospheric CO_2. Climate change is expected to lead directly to changes in distributions of vegetation associations. Distribution of animals will also change to the extent that animals rely on vegetation for food or shelter. Bat species in Texas appear to be restricted, in part, by the availability of roosts. We used geographic information systems and the Holdridge vegetation-climate association scheme to model the effect of climate change on bat distributions and species richness in Texas. Habitat characteristics for each species were identified from the literature and included vegetation, topography, and availability of caves. We assumed caves and topography to be fixed relative to climate. Vegetation changes were predicted from the Holdridge vegetation-climate association scheme. The redistribution of bats following climate change was predicted based on the new locations of suitable habitat characteristics. Under conditions of global warming tropical forests were predicted to expand into Texas; tree-roosting bats were sensitive to this change in vegetation. Cavity-roosting bats were less affected by changes in vegetation, but, where response was predicted, ranges decline.*

El calentamiento global y la riqueza de especies de los murciélagos en Texas

Resumen: *Los modelos de circulación general proveen predicciones climáticas a nivel global, bajo escenarios de incremento en el CO_2 atmosférico. Se espera que los cambios climáticos conduzcan en forma directa a cambios en la distribución de las asociaciones vegetales. Las distribuciones de los animales también cambiarán de acuerdo al grado de dependencia que tengan con respecto a la vegetación como alimento o refugio. Las especies de murciélagos en Texas parecen estar restringidas, en parte, por la disponibilidad de dormideros. En el presente estudio, utilizamos sistemas de información geográficos y el esquema de asociaciones bioclimáticas de Holdridge, para modelar el efecto del cambio climático sobre la distribución y riqueza de especies de murciélagos en Texas. Las características del hábitat para cada especie se obtuvieron a partir de la literatura existente e incluyeron la vegetación, la topografía y la disponibilidad de cuevas. Asumimos que las cuevas y la topografía no varían con respecto al clima. Los cambios de la vegetación fueron predecidos a partir del esquema de asociaciones bioclimáticas de Holdridge. La redistribución de los murciélagos después de a los cambios climáticos fue predecida en base a las nuevas localizaciones de las características apropiadas del hábitat. Bajo condiciones de calentamiento global, se predijo que los bosques tropicales se expanderían dentro de Texas y los murcielagos que duermen en los árboles, se mostraron sensibles a este cambio en la vegetación. Los murciélagos que habitan en cavernas se mostraron menos afectados por los cambios en la vege tación, pero en los casos en que se predijo una respuesta, las áreas de distribución se redujeron.*

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Introduction

Mammals are important both ecologically and economically as prey items, predators, pollinators, seed dispersers, disease reservoirs and vectors, and agricultural pests and products. Because mammals are a taxon diverse in body size, morphology, and ecology, they are not expected to react as a group to environmental shifts such as global climatic change. As part of a larger study of global warming and mammal distributions in Texas (Cameron & Scheel 1993; Cameron & Scheel, unpublished data), we examined the possible response of bat species in Texas to climate change.

Bats have characteristics that make their study important to understanding the impact of climate change on mammals and on society. Worldwide and in Texas, the species richness of bats is exceeded among mammals only by rodents. Bat species may pose minor public health risks in Texas (Schmidly 1991) and provide economically valuable services. For example, bats consume insect pests, are pollinators and seed dispersers, and their guano is collected for fertilizer (Schmidly 1991). Bat communities appear distinctive for being composed of small, long-lived, and slowly reproducing animals, apparently adapted to stable environments (Findley 1993). As the only flying mammals bats may have more flexibility than other mammalian taxa to relocate as a response to climate change. Finally, Findley (1993) suggests that patterns of species richness in bat communities are paralleled by similar patterns in plants, birds, rodents, and fish. Hence, these patterns are likely to reflect processes that are of broad importance in regulating diversity.

Roosts are one of the most important limiting resources for bats, influencing social behavior (Hill & Smith 1984), population size (Hill & Smith 1984), and community diversity (Humphrey 1975; Findley 1993). Typical roosts include caves, rock crevices, buildings, and trees. Because the distribution of trees is sensitive to climate change (Davis 1990) but the distribution of caves and rock crevices remains relatively fixed, the response of bats to global climate change should depend on roost requirements.

Characteristic associations between bats and types of vegetation are not determined solely by roost requirements. Distributions of bats are generally not closely correlated with distributions of particular food species (Willig & Mares 1989) because bats rarely specialize on particular plant or insect taxa (Schmidly 1991). Characteristic habitats are readily identifiable for many bat species (e.g. Schmidly 1991), however, and thus bats may be affected if plant communities respond to climate change. Because of the dependence of some bats on vegetation for roosts, this may be particularly true if the physiognomy of vegetation changes, as, for example, when forest becomes grassland.

Global warming is predicted as a direct result of rising levels of CO_2 in the atmosphere. General circulation models (GCMs) predict that global mean surface air temperature will increase and that spatial distribution of rainfall will change, although these models do not agree on the precise distribution or magnitude of such changes (Bradley et al. 1987; Schneider 1993). Climate has a large impact on biological processes, and, hence, rearrangement of existing biological communities is expected as individual animal or plant species respond to climate change (Graham 1992; Webb 1992). Predictions for plant communities include regional-scale movement of forests (Harris & Cropper 1992; Shugart & Smith 1992; Smith et al. 1992) and, therefore, a profound effect on distributions of bats that rely on vegetation also may be expected.

Models

Using an existing vegetation model and GCMs, we predicted the impact of global climate change on the suitability of habitats for bats as determined by the distribution of vegetation. We then used the habitat specificity of each species of bat to predict the impact of global climate change on their ranges and, consequently, on the diversity of bats in Texas. We recognized three broad types of roosting behavior in bats (Table 1): tree, cavity, and generalist roosting. Tree-roosting bats usually roost in trees (beneath bark, on branches, or in foliage) or buildings, but not in caves or rock crevices. Distributions of roosts used by tree-roosting bats are likely to change as a direct result of climate change. Cavity-roosting bats typically roost in caves, rock crevices, or buildings, but not in trees. The distribution of such roosts will not be affected by climate change (although the suitability of roosts may be affected; Tuttle & Stevenson 1978; Richter et al. 1993). Some species of bats typically use both trees and caves or rock crevices and may use buildings as well; we refer to such species as roost generalists. This category includes, for example, species that roost in trees in summer but use caves for winter hibernation.

To predict the ecological effects of climate change we used the geographic information system ARC/INFO (GIS; Starr & Estes 1990) to model distributions of vegetation and bat species throughout Texas. Future climate was predicted from GCMs for specific locations. Plant distributions were assumed to be a function of climate. Bat distributions were determined by location of suitable vegetation and other relevant components of habitat, such as caves and local topography. The habitat requirements of some bats are for specific characteristics of the flora (for example, *Lasiurus intermedius* roosts primarily in Spanish moss throughout much of its range in the United States; see Webster et al. 1980), whereas the requirements of others are specific only for certain structures in the vegetation (such as trees for roosts). Hence,

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Table 1. Habitat criteria and indicators of model success for bat species.

Species[a]	Habitat characteristics: Roost[b]	Relief[c]	Vegetation[d]	Marginal success[e]	Area[f] (× 1000 km²): Suit	Curr	Under	Over
Mormoops megalophylla	C	C	1, 5-8, 10, 13, 15, 16, 18, 20, 26, 27, 29, 38, 43-46	89 (18)	36.2	159.6 (4.41)	2.3 (.003)	125.7 (.181)
Leptonycteris nivalis	C	MC	5, 7, 18, 29	100 (4)	8.3	74.5 (8.98)	2.0 (.003)	68.2 (.098)
Myotis yumanensis	C		1, 5-8, 10, 18, 46	91 (23)	44.9	129.6 (2.89)	6.1 (.009)	90.8 (.131)
Myotis austroriparius	G		3, 30, 31, 36, 38, 39, 41-46	100 (10)	55.0	120.7 (2.19)	0.0 (0)	65.0 (.095)
Myotis velifer	C	C	1, 4-30, 32, 34, 35, 37, 38, 40, 42, 44-46	70 (98)	169.1	172.4 (1.02)	2.8 (.004)	6.1 (.009)
Myotis thysanodes	C		1, 5-8, 13, 14, 18, 29, 40	100 (16)	54.5	146.9 (2.70)	0.0 (0)	92.4 (.133)
Myotis volans	G	M	5-8, 18, 29, 40	100 (8)	3.8	8.3 (2.18)	0.1 (0)	4.6 (.007)
Myotis californicus	G		1, 5-8, 18, 29, 40, 46	100 (15)	50.1	132.3 (2.64)	3.6 (.005)	85.8 (.124)
Myotis ciliolabrum	G	H	1, 5-8, 11, 14, 18, 29, 32, 34, 37, 40, 46	100 (15)	8.2	8.9 (1.09)	0.0 (0)	0.7 (.001)
Lasionycteris noctivagans	T		18, 19, 26, 27, 29-31, 36-42, 44, 46	94 (17)	331.5	369.3 (1.11)	101.9 (.147)	139.7 (.202)
Pipistrellus hesperus	C	H	1, 2, 5-16, 18-21, 26-29, 32, 34, 37, 40, 44-47	95 (55)	13.7	15.2 (1.11)	0.005 (0)	1.6 (.002)
Pipistrellus subflavus	G		10-13, 16-18, 20, 21, 23-27, 30, 31, 33-39, 42, 46	96 (49)	219.5	554.9 (2.53)	14.7 (.021)	350.1 (.505)
Eptesicus fuscus	G		1-9, 11-14, 18, 19, 21-23, 26-46	100 (57)	364.4	572.4 (1.57)	7.1 (.010)	215.1 (.310)
Lasiurus borealis	T		16-20, 23-27, 29-31, 33-38, 40-42, 44, 46	98 (139)	392.2	460.4 (1.17)	71.0 (.102)	139.2 (.201)
Lasiurus seminolus	T		30, 31, 36, 38, 39, 41, 42, 44, 46	97 (37)	71.5	117.2 (1.64)	5.3 (.008)	51.1 (.074)
Lasiurus cinereus	T	+M	16-20, 23-27, 29-31, 33-38, 40-42, 44, 46	93 (59)	392.2	487.6 (1.24)	70.1 (.101)	165.5 (.239)
Lasiurus intermedius	T		16, 17, 20, 23, 25-27, 30, 31, 36, 38, 39, 41, 42, 44, 46	100 (30)	133.7	448.5 (3.35)	1.6 (.002)	316.4 (.456)
Lasiurus ega	T		44, 46	100 (4)	5.7	0 (0.00)	5.7 (.008)	0 (0)
Nycticeius humeralis	T		16, 17, 20, 26, 27, 30, 31, 36-39, 41, 42, 46	94 (68)	167.3	448.5 (2.68)	1.8 (.003)	282.9 (.408)
Euderma maculatum	C	M	1, 7, 29	100 (2)	0.3	7.3 (24.33)	0.1 (0)	7.1 (.010)
Plecotus townsendii	C	HC	1, 2, 5-15, 18, 19, 21, 22, 26-29, 32, 34, 37, 38, 40, 44-46	92 (39)	120.6	155.8 (1.29)	7.1 (.010)	42.3 (.061)
Plecotus rafinesquii	T		30, 31, 36, 41, 42, 46	100 (8)	42.1	117.2 (2.78)	0.0 (0)	75.2 (.108)
Antrozous pallidus	C	HC	1, 5-16, 18-22, 26-29, 32, 34, 37, 38, 40	89 (72)	123.3	168.9 (1.37)	2.9 (.004)	48.4 (.070)
Tadarida brasiliensis	C		all except 47	100 (202)	685.9	693.1 (1.01)	0.0 (0)	7.2 (.010)
Nyctinomops femorosacca	C	M	7, 29	100 (3)	0.4	7.3 (18.25)	0.1 (0)	7.1 (.010)
Nyctinomops macrotis	C		all except 33, 35	100 (16)	423.9	693.1 (1.64)	0.0 (0)	269.2 (.388)
Eumops perotis	C	H	1, 5-7, 10, 13, 15, 18, 26, 29, 44, 47	67 (6)	4.0	13.1 (3.28)	0.3 (0)	9.3 (.013)
Average:				95.2 (39.6)		(3.65)	11.3 (0.016)	98.8 (0.143)

[a] *We did not model five species that have been recorded in Texas (*Choeronycteris mexicana, Diphylla ecaudata, Myotis lucifugus, Myotis septentrionalis, *and* Lasiurus blossevillii*). The species are known within the state from only a single specimen or location.*

[b] *C, commonly roosts in caves, rock crevices, or buildings, but not trees; T, commonly roosts in trees or buildings but not caves or rock crevices; G (generalist), commonly roosts in trees, caves, or rock crevices. Habitat characteristics for each species were determined from the literature (Watkins 1977; O'Farrell & Studier 1980; Webster et al. 1980; Fitch et al. 1981; Kunz 1982; Shump & Shump 1982a, 1982b; Warner & Czaplewski 1984; Wilkins 1987; Hensley & Wilkins 1988; Jones & Manning 1989; Kurta & Baker 1990; Milner et al. 1990; Schmidly 1991; Rezsutek & Cameron 1993).*

[c] *Response to topographic relief: H, restricted to areas of hills or mountains; M, restricted to mountainous areas; +M, utilizes but is not restricted to mountainous areas; C, restricted to counties with caves.*

[d] *Codes are given for Texas Parks & Wildlife associations known to be occupied by each species. See Appendix 2 for key.*

[e] *Marginal success indicates a known occurrence of a species in habitat we identified as suitable based on information from the literature. We used this as a measure of our success at specifying habitat associations. Success is listed as percentage of marginal records encompassed by area identified as suitable habitat (Marginal, $\bar{x} = 95 \pm SE = 0.02\%$). Parentheses indicate the sample size of marginal capture records.*

[f] *Area comparisons indicate how well the model mimics the known distribution of each species. Suit = area identified as suitable habitat using Texas Park & Wildlife vegetation associations; curr = area identified as habitat by the model using current climate and the Holdridge vegetation associations (parentheses indicate proportional change in areal extent from suitable habitat in the previous column); under = area (and proportion) of state identified by the model as unsuitable in which the species does occur (under, $\bar{x} = 1.6 \pm 0.007\%$); over = area (and proportion) of state identified by the model as suitable in which the species does not occur (over, $x = 14.3 \pm 0.03\%$). The total area of Texas used in calculating these proportions was 693,000 km².*

changes in the abundance and composition of plant communities influence the distribution of each species differently.

The Environment

We used two GCMs to predict average temperature and rainfall in Texas under conditions of twice baseline CO_2 ($2 \times CO_2$; baseline CO_2 levels were 300–315 ppm; R. Jenne, personal communication): the Geophysical Fluid Dynamics Laboratory model (GFDLR30) and the Canadian Climate Center Model (CCC; for further details see Cameron & Scheel 1993). These GCMs were selected because their grid size provided more data points in Texas than those of other GCMs. The 40-year mean annual biotemperature (1951–1990, inclusive; average growing season temperature; Holdridge 1967) and mean annual precipitation were calculated for 315 weather stations in Texas (National Weather Service; hereafter referred to as current climate). Current climate was adjusted for each weather station according to predictions of each GCM to generate predicted average conditions at each station. Both models predicted that temperatures will increase by 3–4°C in Texas relative to current conditions. GFDLR30 predicted increased rainfall throughout the state, however, whereas CCC predicted a slight decline in rainfall. Thus, GFDLR30 is both warmer and wetter than the current climate, and CCC is warmer and somewhat drier (predictions of climate models for Texas are presented in more detail in Cameron & Scheel 1993).

We used the Holdridge (1947, 1967) model of climate-vegetation association to model the type of vegetation resulting from current and $2 \times CO_2$ climate conditions. This model predicted distributions of vegetation life zones based on temperature and precipitation and has been used to predict current and future vegetation distribution (Harris & Cropper 1992; Smith et al. 1992). Under both $2 \times CO_2$ scenarios all warm temperate vegetation types were lost (Holdridge associations 10, 13, 15–17; see Appendix I for key to Holdridge associations). For the GFDLR30 (wetter) model, all subtropical vegetation was also lost (Holdridge associations, 1–5, 7, 14) and tropical forests were added (e.g., Holdridge associations 20, 24, 33, 35–36, 39). Under the CCC (drier) climate model, subtropical forest, tropical dry forest, steppe, and desert scrub were added (e.g., Holdridge associations 18, 20–22, 24, 26) because, compared to GFDLR30, the north-south temperature increase was more severe and rainfall decreased (for further details see Cameron & Scheel 1993). We did not model changes in seasonal variability.

Bat Distributions and Species Richness

We digitized the geographic range for each species of bat ($n = 27$) found in Texas (Schmidly 1991). Bats recorded in Texas in a single record only ($n = 5$; Schmidly 1991) were considered vagrants and were not included in these analyses. Published distribution maps represent an upper limit in areal extent for a species' range, and the actual range can be identified as areas of preferred habitat that occur within the larger boundary. We determined the actual distribution of each species by overlaying its geographic range with distributions of those vegetation types or suitable habitats it was known to occupy (Table 1).

Habitat descriptions were used to classify vegetation types occupied by each bat according to a classification by Texas Parks and Wildlife Department (TP&W; McMahan et al. 1984) as described in Cameron and Scheel (1993). In addition to vegetation, habitat criteria for some species of bats included presence of caves or topographic relief (hills, river gorges, mountains) utilized for roosts (Table 1). Bats that roosted in caves were assumed to be restricted to counties with at least one known bat cave (Fig. 1; Elliott 1987). Bats requiring topographic relief were assumed to be restricted to areas of hills (defined as at least 200 m elevation change within a 1000-km^2 area at 400–800 m above sea level) or mountains (defined as at least a 200 m elevation change within a 100-km^2 area above 800 m). These definitions of relief successfully delineated the hill country of west-central Texas and the mountains of the Trans-Pecos region, including the Guadelupe, Davis, Tierra Vieja, and Chisos Mountains. For each bat species we compared locations of marginal capture records in the range (Hall 1981) with locations of suitable habitat, based on the above criteria. Finally, we overlaid distribution maps for all species and, within each area of overlap, counted the number of species present to determine species richness.

We predicted the distribution of each bat species under current and $2 \times CO_2$ climates using the Holdridge (1947, 1967) model of vegetation distribution. It was necessary first to identify characteristic habitat(s) of each species under the Holdridge vegetation classification. Therefore, each TP&W association was identified with one to six Holdridge vegetation associations that overlapped it to the greatest extent and that had comparable physiognomy (Cameron & Scheel 1993; Appendix II). Some TP&W associations were not matched to any Holdridge association because no comparable Holdridge type existed (e.g., crops, urban areas, wetlands) or because the association was limited to less than 0.5% of the area of the state. Suitable Holdridge habitats for a bat species that used an unmatched TP&W association were identified through other suitable TP&W associations (i.e., bats used more than one TP&W association). To predict distributions of bats for Holdridge models of vegetation, each species was assigned to occur in those Holdridge associations that were identified as similar to TP&W vegetation types in which it was known to occur. Where appropriate, modeled ranges were then corrected for the presence of caves or topographic relief.

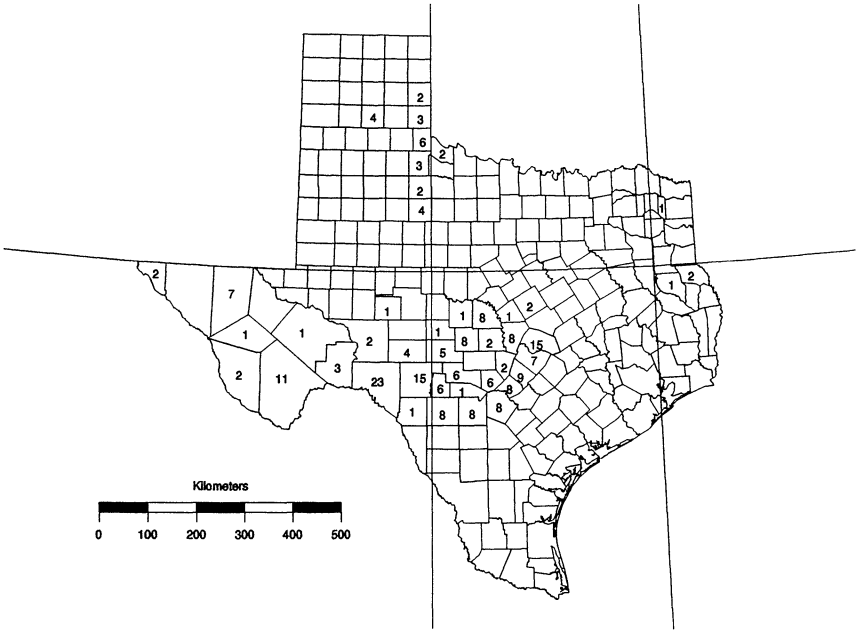

Figure 1. Distribution of known bat caves in Texas counties (Elliott 1987). Counties without numbers have no known bat caves. County map digitized from USGS 1 : 1,000,000 base map.

To estimate the success of our model at predicting the distribution of bats, we asked two questions: How well did we identify the TP&W vegetation associations where bats were found? How well does the model mimic bat distributions under current climate conditions? The first question targets our knowledge of the habitat associations of bats; the second asks how well the model can mimic reality. We calculated our success at identifying appropriate TP&W habitat as the percentage of marginal capture records located in TP&W habitats selected as suitable for a species (Table 1). We estimated the success of the model in predicting distributions for each species by comparing actual distribution (areas of TP&W associations identified as suitable within a species' range) with modeled distribution (areas of suitable Holdridge habitats) under current climate conditions. For this comparison we provide three values (Table 1): the relative areal extent of the modeled range to the TP&W range, and two measures of the proportion of the study area incorrectly identified by the model for each species (calculated as the ratio of total area within Texas incorrectly identified to total area of the state). Areas incorrectly identified were either undershoots—occupied by a species but predicted to be unoccupied—or overshoots—unoccupied by a species but predicted to be occupied. We based the comparison of actual with modeled distributions on total area of the state rather than on the current or predicted range of a species to fix our maximum error at 1.0 and to avoid results biased by the size of each range. This allowed comparisons among species and roost types to be made.

Some Holdridge vegetation types did not occur under the current climate but did occur under 2 × CO_2 climates. We could not identify these associations with a TP&W vegetation association based on overlap as described above. Instead, we either (1) designated them as suitable habitat for a species based on descriptions of the habitat of each species taken from the literature (Cameron & Scheel 1993) or (2) matched them with similar Holdridge associations that did occur under current climate. For example, animals utilizing "warm-temperate moist forest" based on TP&W-Holdridge overlap were predicted to use "subtropical moist forest," which occurred only under 2 × CO_2 climates. We assigned most bats to at least one Holdridge vegetation type that did not occur currently in the state, but was predicted to occur under 2 × CO_2. This is equivalent to assuming that these bats can utilize a broader spectrum of habitats than are present within the state (as depicted by TP&W). Although matching vegetation outside of Texas to Holdridge vegetation types is outside the scope of this study, our assumption that bats can use more habitats than found within Texas is supported by the fact that all bats that occur in Texas (Schmidly 1991) also occur outside the state (Hall 1981).

Species distributions under 2 × CO_2 were modeled using the same procedure as under current conditions. Climate change was assumed to alter vegetation distribution only. Species preferences for habitats and roosts were assumed to be fixed (except as noted above for newly arrived vegetation associations) with respect to the time scale of climate change. We predicted that a species would become extinct in Texas when no suitable habitat occurred in the state. Some of the species may move into adjacent states along with preferred habitats, but, because of the geographic limit to our study,

we recorded such movement as a local extinction. All ranges were overlain to produce a distribution of species richness as predicted by the Holdridge model for each climatic model. ANOVA statistics comparing proportions were done on arcsine transformations of the data using SYSTAT statistics software (Wilkinson 1990).

Assumptions and Limitations

Critical elements of our analyses were the dependence of vegetation on climate and the dependence of bats on the presence of suitable habitat features. Our assumption that plant communities would respond intact to climate change is shared by other schemes that use precipitation and temperature as primary axes along which to classify plant communities (Orians 1993), as well as by models used to predict the effects of global climate change on plant communities (Shugart & Smith 1992; Smith et al. 1992). Although an increased understanding of mechanisms that regulate plant physiology and physiognomy, such as soil texture and water potential, is leading to development of mechanistic models of plant communities (Woodward 1987; R. P. Neilson, 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecological Applications.), such models do not alter the assumption that plant communities remain intact as climate shifts. As a cautionary note, there is strong evidence that plant species can respond individually to changes in climate (Davis 1984).

We also assume that habitat and roost specificity are important limitations to bat distributions. We recognize that other factors, such as severity or frequency of abiotic variables, availability of food, competition, or predation, also may limit distributions, but data on the responses of bats to these factors are less available than information on habitat and roost specificity.

Habitat associations for most species are better documented than the mechanisms that lead to restriction of a

Table 2. Area (x 1000 km^2) of habitat predicted for bat species occurring in Texas.

		Suitable habitat[a]			*Overlap*[b]		*New associations*[c]	
Species	*Roost type*[d]	*Current*	*CCC*	*GFDLR30*	*CCC*	*GFDLR30*	*CCC*	*GFDLR30*
Mormoops megalophylla	cavity	159.6	134.9 (0.85)	102.7 (0.64)	129.4 (0.96)	95.4 (0.93)	42.5 (0.32)	42.3 (0.41)
Leptonycteris nivalis	cavity	74.5	69.5 (0.93)	63.2 (0.85)	59.8 (0.86)	36.0 (0.57)	17.3 (0.25)	11.9 (0.19)
Myotis yumanensis	cavity	129.6	278.6 (2.15)	124.5 (0.96)	86.5 (0.31)	45.3 (0.36)	134.9 (0.48)	61.3 (0.49)
Myotis austroriparius	generalist	120.7	89.4 (0.74)	279.9 (2.32)	89.4 (1.00)	117.2 (0.42)	89.4 (1.00)	279.9 (1.00)
Myotis velifer	cavity	172.4	172.4 (1.00)	172.4 (1.00)	172.4 (1.00)	172.4 (1.00)	71.8 (0.42)	112.1 (0.65)
Myotis thysanodes	cavity	146.9	339.7 (2.31)	267.5 (1.82)	110.5 (0.33)	86.2 (0.32)	175.7 (0.52)	77.4 (0.29)
Myotis volans	generalist	8.3	6.6 (0.80)	8.5 (1.02)	6.2 (0.94)	7.8 (0.92)	2.3 (0.35)	0.8 (0.09)
Myotis californicus	generalist	132.3	286.3 (2.16)	251.4 (1.90)	89.1 (0.31)	61.7 (0.25)	134.9 (0.47)	61.3 (0.24)
Myotis ciliolabrum	generalist	8.9	8.9 (1.00)	8.5 (0.96)	8.9 (1.00)	8.5 (1.00)	2.3 (0.26)	0.8 (0.09)
Lasionycteris noctivagans	tree	369.3	287.1 (0.78)	495.4 (1.34)	208.4 (0.73)	347.0 (0.70)	201.9 (0.70)	347.7 (0.70)
Pipistrellus hesperus	cavity	15.2	15.2 (1.00)	13.8 (0.91)	14.7 (0.97)	13.8 (1.00)	4.7 (0.31)	3.9 (0.28)
Pipistrellus subflavus	generalist	554.9	568.4 (1.02)	499.9 (0.90)	513.9 (0.90)	458.8 (0.92)	389.4 (0.69)	475.9 (0.95)
Eptesicus fuscus	generalist	572.4	506.6 (0.89)	568.4 (0.99)	392.1 (0.77)	506.9 (0.89)	265.1 (0.52)	357.3 (0.63)
Lasiurus borealis	tree	460.4	518.8 (1.13)	625.5 (1.36)	445.5 (0.86)	460.4 (0.74)	376.9 (0.73)	477.7 (0.76)
Lasiurus seminolus	tree	117.2	89.4 (0.76)	279.9 (2.39)	89.4 (1.00)	117.2 (0.42)	89.4 (1.00)	279.9 (1.00)
Lasiurus cinereus	tree	487.6	546.9 (1.12)	651.9 (1.34)	474.0 (0.87)	487.6 (0.75)	378.8 (0.69)	478.2 (0.73)
Lasiurus intermedius	tree	448.5	511.1 (1.14)	498.7 (1.11)	433.9 (0.85)	392.0 (0.79)	376.9 (0.74)	477.7 (0.96)
Lasiurus ega	tree	0	0	6.2	0	0 0.00	0	6.2 (1.00)
Nycticeius humeralis	tree	448.5	511.1 (1.14)	498.7 (1.11)	433.9 (0.85)	392.0 (0.79)	376.9 (0.74)	477.7 (0.96)
Euderma maculatum	cavity	7.3	4.9 (0.67)	7.5 (1.03)	4.6 (0.94)	6.0 (0.80)	1.9 (0.39)	0.8 (0.11)
Plecotus townsendii	cavity	155.8	126.0 (0.81)	78.0 (0.50)	113.4 (0.90)	78.0 (1.00)	30.8 (0.24)	15.4 (0.20)
Plecotus rafinesquii	tree	117.2	89.4 (0.76)	279.9 (2.39)	89.4 (1.00)	117.2 (0.42)	89.4 (1.00)	279.9 (1.00)
Antrozous pallidus	cavity	168.9	143.4 (0.85)	105.4 (0.62)	142.0 (0.99)	104.0 (0.99)	43.8 (0.31)	42.8 (0.41)
Tadarida brasiliensis	cavity	693.1	693.1 (1.00)	693.1 (1.00)	693.1 (1.00)	693.1 (1.00)	390.6 (0.56)	482.1 (0.70)
Nyctinomops femorosacca	cavity	7.3	4.9 (0.67)	7.5 (1.03)	4.6 (0.94)	6.0 (0.80)	1.9 (0.39)	0.8 (0.11)
Nyctinomops macrotis	cavity	693.1	693.1 (1.00)	693.1 (1.00)	693.1 (1.00)	693.1 (1.00)	390.6 (0.56)	482.1 (0.70)
Eumops perotis	cavity	13.1	10.1 (0.77)	11.7 (0.89)	9.7 (0.96)	9.7 (0.83)	3.4 (0.34)	2.2 (0.19)
Averages:			1.05	1.21	0.86	0.73	0.54	0.55

[a] *Area of habitat predicted by our model under the current climate (Current), the Geophysical Fluid Dynamics Laboratory model (GFDLR30), and the Canadian Cimate Center model (CCC). Parentheses indicate extent of habitat under each predicted climate relative to current climate model.*

[b] *Area of habitat that overlaps the extent of the range under current climate. Parentheses indicate extent of overlap relative to total area for each predicted climate. CCC and GFDLR30 as for suitable habitat.*

[c] *Area of habitat that is composed of Holdridge vegetation associations not found in the state under current climate. Parentheses indicate extent of new associations relative to total area under each predicted climate. CCC and GFDLR30 as for suitable habitat.*

[d] *See Table 1 for roost type definitions.*

species to particular habitats. For this reason, although it is impractical to build a model using mechanisms of habitat use for an entire taxa, we were able to use habitat associations. The predictive value of habitat associations varies among species: some bats have general vegetation specificities (e.g., *Nyctinimops macrotis*; Table 1) whereas others are limited in the habitats they use (e.g., *Lasiurus ega*). But bat distributions are known to respond to changes in the distribution of the vegetation upon which they rely. For example, *L. ega* has apparently expanded its range into California, Arizona, New Mexico, and Texas in response to the introduction of ornamental palms into these states (Schmidly 1991). Furthermore, it is generally accepted that bats may be roost-limited. Artificial roosts have been used in Texas since the early 1900s to increase bat numbers, although the success of these efforts has been disputed (Schmidly 1991). Findley (1993) concludes that bat communities are organized primarily by their responses to resources (vegetation, roosts) and to historic and geographic factors (species distributions and caves or terrain). Our model includes these as major predictors of bat distributions.

Finally, the spatial resolution of our model is coarse because the Holdridge model uses only temperature and precipitation to predict vegetation. As in other models of vegetation-climate associations, the Holdridge model predicted plant communities that would appear under particular climates if vegetation and climate were in equilibrium. In fact, even in the absence of rapid climate change, land use by humans affects this equilibrium, resulting in a mismatch between actual and modeled vegetation (Cameron & Scheel 1993).

Results

Species Distributions

Lasiurus ega, the southern yellow bat, was the only bat not predicted to occur in the state under current conditions; this species roosts most often in ornamental palm trees in southern Texas. Statistics on the success of the model (Table I) included *L. ega* and thus were based on $n = 27$ species, whereas statistics on the effects of climate change (Table 2) do not include *L. ega* and were based on $n = 26$. Areas we categorized as suitable encompassed, on average, 95% of the capture points for a species (marginal success, Table 1), indicating that we successfully identified TP&W habitats used by a species. On average 84.1% of the area of the state was correctly identified by the model as included in or excluded from ranges of the species ($n = 27$). Overshoot errors were more extensive than undershoots, and on average the modeled range was 3.65 times the area of the TP&W habitat selected as suitable (area, Table 1). When bat species were categorized according to roost type (Table 1), total errors (overshoots plus undershoots) for roost generalists and tree specialists appeared higher than for cavity specialists, but these differences were not significant (ANOVA, $F = 3.129$, $df = 2$, $p = 0.062$). The average error (overshoots plus undershoots; $\bar{x} = 0.159 \pm \text{SE} = 0.030$, $n = 27$ species) for bats was the lowest of four orders we have modeled (the other three were insectivores: $\bar{x} = 0.28 \pm 0.08$, $n = 4$; lagomorphs: $\bar{x} = 0.22 \pm 0.08$, $n = 4$ (Cameron & Scheel 1993); and rodents: $\bar{x} = 0.24 \pm 0.02$, $n = 58$ (Cameron & Scheel, unpublished data).

Under both 2 × CO_2 climates, average range size was predicted to increase slightly relatively to current modeled range sizes (Table 2, ratio of 2 × CO_2 range size to current modeled range size for CCC: $\bar{x} = 1.05 \pm 0.09$; GFDLR30: $\bar{x} = 1.21 \pm 0.10$, $n = 26$; *L. ega* excluded). Although average range size was predicted to increase

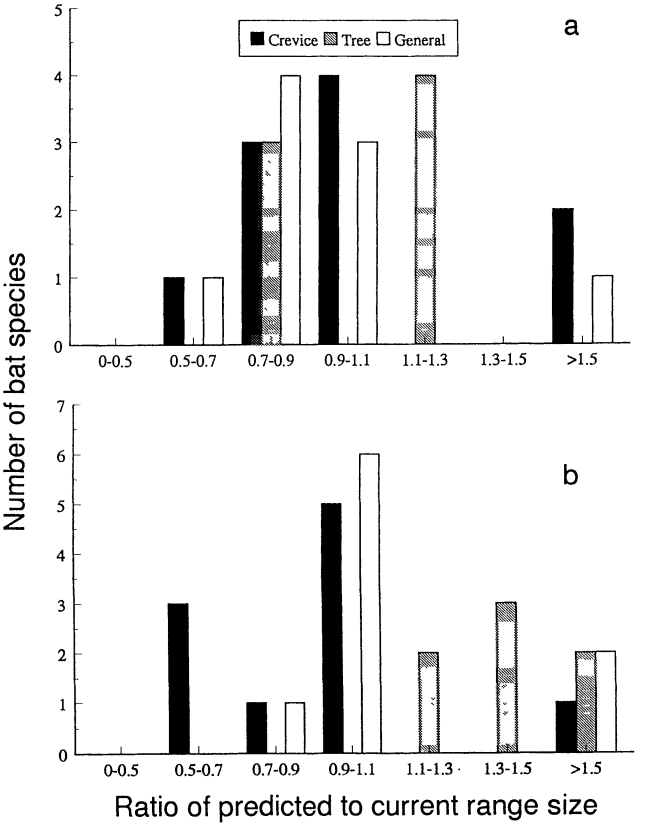

Figure 2. Extent of species ranges following climate change relative to extent of range modeled under current climate for the change predicted by global climate models of the Canadian Climate Centre (CCC) (a) and the Geophysical Fluid Dynamics Laboratory (GFDLR30) (b). Ratios larger than 1 indicate that the range is predicted to expand following climate change, ratios equal to 1 indicate no change, and ratios smaller than 1 indicate contraction of the range.

under each 2 × CO_2 climate, large increases for three species (*Myotis yumanensis*, *M. thysanodes*, *M. californicus*) heavily influenced the average under the CCC (drier) climate. For that climate 13 of the 26 modeled species were predicted to decrease slightly in range size, five remained unchanged, and only eight species increased in geographic extent (Fig. 2a). In contrast, under the GFDLR30 (wetter) climate half of the 26 species were predicted to increase their range size, three remained unchanged, and 10 decreased in extent. For the GFDLR30 climate, tree-roosting and roost-generalist species increased in extent relative to current conditions significantly more than cavity-roosting bats (Fig. 2b: cavity, $\bar{x}$ = 0.94; tree, $\bar{x}$ = 1.58; generalists, $\bar{x}$ = 1.35. ANOVA: $F = 4.6$, $df = 2, p = 0.021$). Differences for the CCC model were not significant (cavity, $\bar{x}$ = 1.08; tree, $\bar{x}$ = 0.98; generalists, $\bar{x}$ = 1.10. ANOVA: $F = 0.14$, $df = 2$, $p = 0.86$).

The geographic ranges of species moved as well as changed in extent. We examined movement of ranges by calculating the proportion of the ranges under 2 × CO_2 climate that overlapped modeled ranges under current climate: high overlap indicated little movement (Table 2). Although overlaps ranged from zero to 100%, on average, species did not move much, and ranges under 2 × CO_2 climate overlapped ranges under current conditions by 75–85% (CCC: $\bar{x}$ = 0.86 ± 0.04; GFDLR30: $\bar{x}$ = 0.73 ± 0.05, n = 26). Larger movements may have been obscured because our study was limited in geographic extent to the state of Texas. There were no differences in movement of ranges between bats using different roost types (CCC: ANOVA: $F = 0.62$, $df = 2, p = 0.94$; GFDLR30: $F = 2.9$, $df = 2, p = 0.07$).

We assumed that bats under 2 × CO_2 climates would utilize some new vegetation types that did not occur under the current climate within Texas, and, hence, were not available under current conditions. The effect of this assumption was indicated by the proportion of the range of each species that was comprised of new vegetation types under each 2 × CO_2 climate (Table 2). On average 50% of 2 × CO_2 ranges were composed of new habitat types (CCC: $\bar{x}$ = 0.54 ± 0.05, n = 26; GFDLR30: $\bar{x}$ = 0.55 ± 0.06, n = 27). Under both 2 × CO_2 climates the ranges of tree-roosting bats included a significantly higher proportion of new vegetation types than did those of cavity-roosting bats or roost generalists (ANOVA, CCC: $F = 10.0$, $df = 2, p = 0.001$; GFDLR30: $F = 10.8$, $df = 2, p < 0.001$; cavity-roosting bats CCC: $\bar{x}$ = 0.39 ± 0.03, n = 13; GFDLR30: $\bar{x}$ = 0.36 ± 0.06, n = 13; generalist-roosting bats CCC: $\bar{x}$ = 0.55 ± 0.10, n = 6; GFDLR30: $\bar{x}$ = 0.50 ± 0.16, n = 6; tree-roosting bats CCC: $\bar{x}$ = 0.80 ± 0.05, n = 8; GFDLR30: $\bar{x}$ = 0.89 ± 0.04, n = 9). Bats may not be as flexible in their habitat as we have assumed, and therefore those species utilizing largely new vegetation types under 2 × CO_2 climates may be at high risk of decline or extinction in Texas.

Species Richness

Modeled species richness of chiropterans was low in the central part of Texas and higher in the east and west. Areas of highest diversity were in the western mountains (Fig. 3a). This pattern reflected the actual gradients of bat species richness in the state (Humphrey 1975; Owen 1990), although modeled diversity was in general higher than actual diversity). This occurred because ranges of

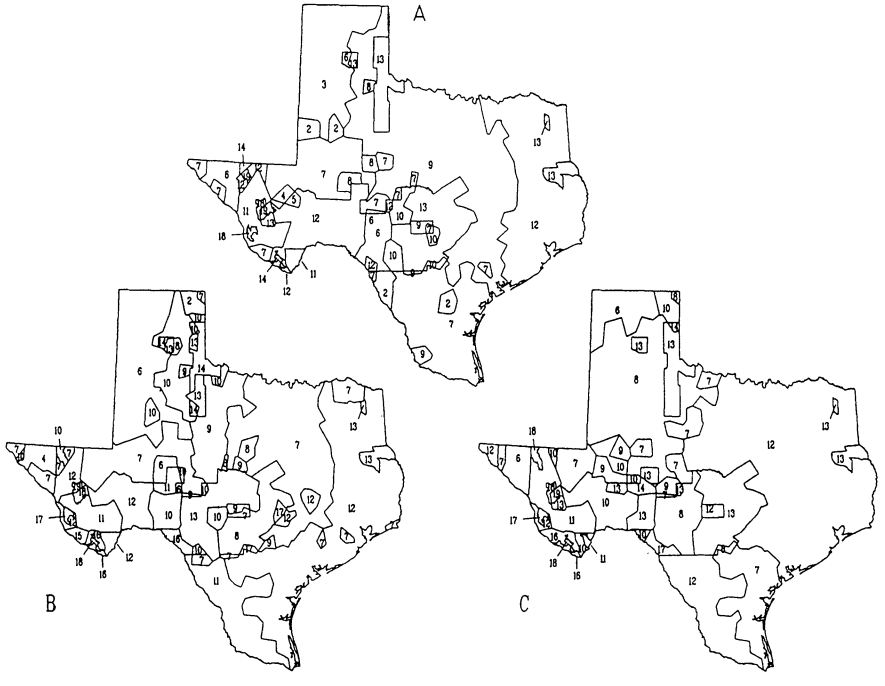

Figure 3. Chiropteran species richness in Texas as predicted by models under current climate (a) and following climate change predicted by the global climate models of the Canadian Climate Centre (b) and the Geophysical Fluid Dynamics Laboratory (c). Numbers indicate the number of species present in each area.

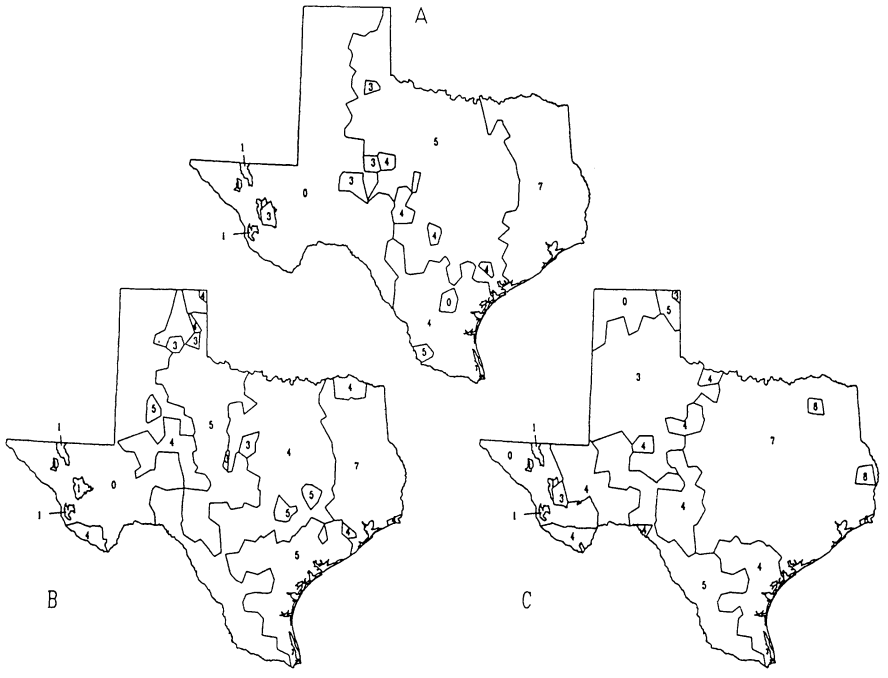

Figure 4. Species richness of tree-roosting bats in Texas as predicted by models under current climate (a) and following climate change predicted by the global climate models of the Canadian Climate Centre (b) and the Geophysical Fluid Dynamics Laboratory (c). Numbers indicate the number of species present in each area.

species were on average overshot by the model. Thus, more species are predicted to occupy central Texas than actually do.

In southern and central Texas species richness increased under both 2 × CO_2 climates (Fig. 3b & 3c) because tree-roosting bats expanded into central portions of the state, the panhandle, and southern Texas (Fig. 4). Although present under both 2 × CO_2 climates, this trend was much stronger in the GFDLR30 (wetter) model than in the CCC model (the extent of forests increased under GFDLR30 more than under CCC).

The species richness of cavity-roosting bats in the central-hill area declined from six species to three in the GFDLR30 climate, and species richness in a large portion of the trans-Pecos region declined from nine cavity-roosting species to five (Fig. 5a & 5c). Although the number of cavity-roosting species inhabiting the central-hills portion of the state declined, total species richness

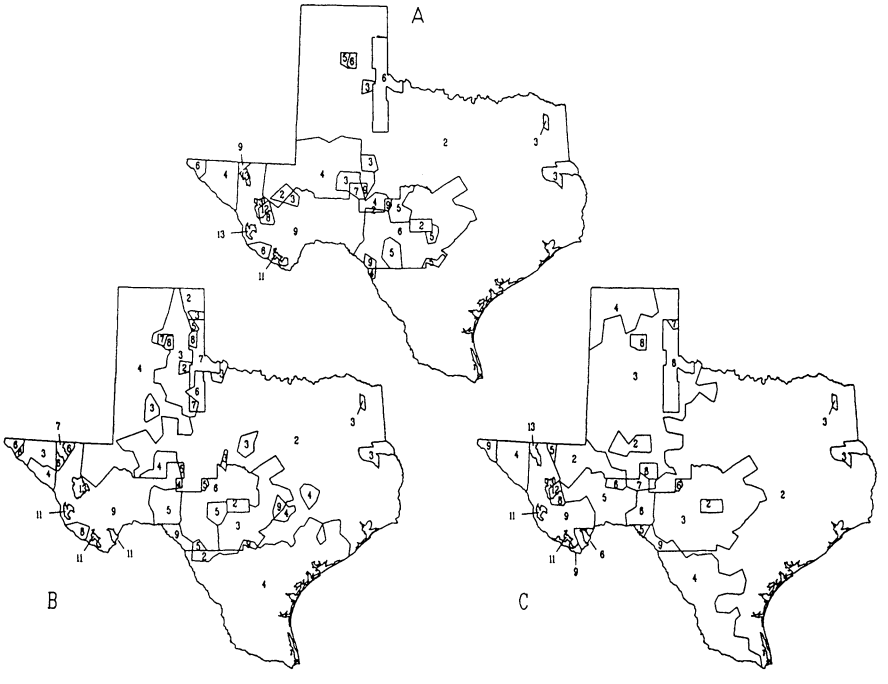

Figure 5. Species richness of cavity-roosting bats in Texas as predicted by models under current climate (a) and following climate change predicted by the global climate models of the Canadian Climate Centre (b) and the Geophysical Fluid Dynamics Laboratory (c). Numbers indicate the number of species present in each area.

did not decrease there because tree-roosting bats expanded their ranges into this area (especially under GFDLR30; Fig. 4a & 4c). Species richness in west Texas generally did not increase because of the loss of cavity-roosting bats (Fig. 3). Finally, roost generalists showed a slight increase only under the GFDLR30 climate, and changes for roost generalists were less extensive than for cavity- or tree-roosting bats.

Discussion

Under conditions of global warming all warm temperate vegetation is predicted to be lost from Texas and replaced either with tropical forests under GFDLR30 (wetter) climate or subtropical forest, tropical dry forest, steppe, and desert scrub under CCC (drier) climate (Cameron & Scheel 1993). We predicted that bats in Texas would respond to changes in climate and vegetation with movement and changes in the geographic extent of species' ranges. We predicted no extinctions within the state as a result of climate change, although one species that occurs in Texas currently (*Lasiurus ega*; Table 1) was not predicted to do so by the model under current climate conditions.

Ranges of tree-roosting and roost-generalist bats expanded as tropical and subtropical forests and woodlands increased or moved into the state. Forest increase was greatest under the wetter of the two climate models we examined (GFDLR30), and, under this climate, all tree-roosting species increased their range (Fig. 2b). *Myotis austroriparius*, a roost-generalist species that uses forest habitat, also increased its range under this climate. *Lasiurus ega* is a Neotropical bat that appears to be expanding its range from Mexico into California, Arizona, and Texas because of increased usage of ornamental palms in landscaping (Schmidly 1991). Although the model did not indicate the presence of *L. ega* under current conditions in Texas, this bat was predicted to enter Texas as climate becomes warmer and wetter. Other bats that currently use tropical forests south of Texas may move north, as was predicted for *L. ega*, thereby increasing species diversity. We were unable to model this movement because our database did not extend into Mexico, but of the more than 100 species of bats in Mexico, only 27 have ranges currently extending into Texas (Hall 1981). This suggests a large potential for movement of new species into Texas. But it is also possible that because species richness of chiropterans was predicted to increase in south Texas under either $2 \times CO_2$ climate (Fig. 3b and 3c), competition between species moving south into new forests and species moving north from Mexico may play an important role in determining final community composition.

Successful expansion of tree-roosting bats into new areas depends on our assumption that these bats can utilize new tree associations that were predicted to occur in Texas as a result of climate change (new associations, Table 2). Bats may not be as flexible as we have assumed. Some tree-roosting bats in Texas (such as *Lasionycteris noctivagans*) are found primarily in northern latitudes (Hall 1981), suggesting that utilization of tropical forests may be inappropriate for such species.

Ranges for cavity-roosting bats decreased as suitable vegetation found near caves and in mountainous terrain under current climate was replaced by unsuitable vegetation under GFDLR30. This replacement resulted in a decline in areas where vegetation and suitable roosts co-occurred for these bats (e.g., *Mormoops megalophylla*, *Plecotus townsendii*, and *Antrozous pallidus*). Some species expanded their ranges under the CCC (drier) climate (e.g., *Myotis yumanensis*, *M. thysanodes*, and *M. californicus*). These bats typically used semiarid habitats in west Texas and were not limited in roost type to caves. Thus, as dry habitats expanded under the CCC climate, these bats were predicted to use larger areas of the state.

Stokes and Slade (1994) note that rodents using drought-induced cracks in the soil have more stable populations in the face of drought than populations unable to utilize cracks in the soil for refuge. We also predicted less change in the distribution of crevice-roosting bats following climate change; although, where change occurred, it was more likely to be a decrease in range relative to the current climate. This was a result of modeling fixed roosts as a critical component of habitat for these bats. These conclusions and those of Stokes and Slade (1994) emphasize the importance of considering shelter and topography in addition to top-down and bottom-up factors when predicting the impact of climate change on animal populations.

Bats that depend on fixed roosts for hibernacula or maternity shelters may be particularly sensitive to climate change that shifts foraging habitat (vegetation associations) away from these roosts. Cavity-roosting bats are sensitive to microclimate in hibernacula (Richter et al. 1993) and maternity roosts (Tuttle & Stevenson 1978; Findley 1993; Lewis 1993). There is reason to expect that climate change will affect microclimate in caves and crevices because internal cave temperature responds to both mean annual surface temperature and seasonal variation in surface-air temperature (Tuttle & Stevenson 1978; Richter et al. 1993). Many roosting areas provide a range of microclimates from which bats may choose (Tuttle & Stevenson 1978), possibly allowing for the continued existence of suitable roosting areas following climate change, particularly in large and structurally complex caves. We are unable to model these conditions because relationships between climate and roost conditions are generally unknown, as are tolerances of different bat species to roost microclimate. Many cave-roosting bats within the United States are roost limited,

however, because most U.S. caves are too warm in the winter for use as hibernacula by bats and too cool in the summer for use as nurseries (Tuttle & Stevenson 1978). In the face of movement of suitable vegetation away from geographically fixed roosts, as well as climate-induced shifts in roost microclimate, cavity-roosting bats—particularly hibernating bats—may be adversely affected by climate change.

Predictions from our models incorporated species-specific responses to changes in the distribution of critical habitat components. By analyzing responses of the entire bat community of Texas to climate change, we hoped to see what might be done in general to prevent the decline of mammalian biodiversity in the face of human-caused climate change. Our study suggested that both forest and cave management potentially can influence bat diversity. The Holdridge vegetation model (Holdridge 1947, 1967) predicted vegetation communities under an assumption of climate-vegetation equilibrium that is unlikely to occur because of human demands on natural resources. Our study demonstrates that increasing forested areas may be necessary to maintain the species richness of bats under global climate change. For bats to benefit from new habitat, however, areas must be set aside where suitable forests can mature. Young forests may not provide suitable roost sites for many tree-roosting species, so there may be a lag of years or centuries before a newly forested area can support a diverse bat community. Current parks in the state preserve areas of forested land (e.g., Big Thicket National Preserve, Guadelupe Mountains National Park). But such preserved lands are concentrated in the eastern forests and western mountains of the state, and little land is set aside in southcentral Texas, where the ranges of bats are predicted to expand the most.

Cave-roosting bats face a particular difficulty because preferred vegetation moves, whereas roosts remain fixed. Adequate protection of caves from human disturbance would, therefore, be crucial to protecting the diversity of bats over the course of global climate change. Efforts at protection should be focused on structurally diverse caves that are likely to provide the greatest range of microclimates for roosting sites, even if such caves are not currently used heavily by bats (Tuttle & Stevenson 1978). Unfortunately for cavity-roosting bats, there may be little that management can do to prevent losses of particular types of preferred vegetation near cave locations.

Predicted climate change, by itself, does not appear to present a grave threat to the species richness of bats in Texas. No bats were predicted to go extinct, and species richness may, in fact, increase substantially through the expansion of species ranges both within Texas and into Texas from Mexico. Sufficient bat populations, caves, forest stands, and other roost types must remain available, however, to allow bat populations to respond to their changing world.

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Appendix 1

Holdridge associations occurring in Texas (from Cameron & Scheel 1993).

1	Subtropical lower-montane dry forest
2	Subtropical thorn woodland-dry forest transition
3	Subtropical dry forest
4	Subtropical lower-montane thorn steppe-dry forest transition
5	Subtropical lower-montane thorn steppe
6	Tropical lower-montane thorn steppe
7	Subtropical lower-montane desert scrub
8	Tropical premontane desert scrub-thorn woodland transition
9	Tropical lower-montane desert scrub
10	Warm temperature moist forest
11	Tropical premontane thorn woodland-dry forest transition
12	Tropical lower montane dry forest
13	Warm temperate dry forest
14	Subtropical lower-montane desert scrub-thorn steppe transition
15	Warm temperate thorn steppe-dry forest transition
16	Warm temperate dry forest-moist forest transition
17	Warm temperate thorn steppe
18	Subtropical dry forest-moist forest transition
19	Subtropical lower montane dry forest-moist forest transition
20	Tropical premontane thorn woodland
21	Tropical thorn woodland-very dry forest transition
22	Tropical very dry forest
23	Tropical very dry forest-dry forest transition
24	Tropical premontane dry forest
25	Tropical lower-montane desert scrub-thorn scrub transition
26	Tropical lower-montane thorn steppe-dry forest transition
27	Subtropical moist forest
28	Subtropical thorn woodland
29	Subtropical lower-montane moist forest
30	Tropical premontane desert scrub
31	Tropical desert scrub-thorn woodland transition
32	Tropical thorn woodland
33	Tropical dry forest
34	Tropical dry forest-moist forest transition
35	Tropical premontane dry forest-moist forest transition
36	Tropical premontane moist forest
37	Tropical premontane moist forest-wet forest transition
38	Tropical lower-montane dry forest-moist forest transition
39	Tropical lower-montane moist forest
40	Tropical lower-montane moist forest-wet forest transition

Appendix 2

Texas Parks & Wildlife vegetation associations matched to similar Holdridge associations.*

Texas Parks & Wildlife Association	*Similar Holdridge associations*
1 Tobosa-Black Grama Grassland	6
2 Blue Grama-Buffalograss Grassland	15
3 Bluestem Grassland	14
4 Silver-Bluestem-Texas Wintergrass Grassland	14
5 Yucca-Ocotillo shrub	8
6 Creosotebush-Tarbush shrub	5, 25
7 Creosotebush-Lechuguilla shrub	5, 6, 25
8 Creosotebush-Mesquite shrub	7, 30, 31
9 Fourwing Saltbush-Creosotebush Shrub	none
10 Ceniza-Blackbrush-Creosotebush Brush	8
11 Mesquite Brush-Mesquite Shrub/Grassland	5, 25
12 Mesquite Lotebush Shrub/Brush	17, 26
13 Mesquite-Juniper Shrub/Live Oak Brush	17, 26
14 Mesquite-Sandsage Shrub	7, 9, 25, 30, 31
15 Mesquite-Blackbrush Brush	4
16 Mesquite-Granjeno Parks	2, 20, 28
17 Mesquite-Granjeno Woods	3, 24, 26, 31, 33
18 Mesquite-Saltcedar Brush/Woods	none
19 Mesquite-Hackberry Brush/Woods	25
20 Mesquite-Live Oak-Bluewood Parks	1
21 Havard Shin Oak-Mesquite Brush	5
22 Sandsage-Mesquite Brush	none
23 Oak-Mesquite-Juniper Parks/Woods	13
24 Live Oak-Mesquite Parks	11
25 Live Oak Woods/Parks	3, 24, 26, 31, 33
26 Live Oak-Mesquite-Ashe Juniper Parks	13
27 Live Oak-Juniper Woods	10
28 Havard Shin Oak Brush	none
29 Gray Oak-Pinyon Pine-Alligator Juniper Parks/Woods	12
30 Post Oak Woods, Forest, and Grassland Mosaic	16, 18, 19, 34, 35, 38
31 Willow Oak-Water Oak-Blackgum Forest	10, 27, 29, 36, 39
32 Sandsage-Havard Shin Oak Brush	15
33 Ashe Juniper Parks/Woods	none
34 Juniper-Mixed Brush	none
35 Elm-Hackberry Parks/Woods	none
36 Water Oak-Elm Hackberry Forest	16, 18, 19, 26, 34, 35
37 Cottonwood-Hackberry-Saltceder Brush/Woods	none
38 Pecan-Elm Forest	none
39 Bald Cypress-Water Tupelo Swamp	none
40 Ponderosa Pine-Douglas Fir Parks/Forest	none
41 Young Forest/Grassland	none
42 Pine-Hardwood Forest	9, 18, 29, 35, 38
43 Marsh/Barrier Islands	none
44 Crops	none
45 Other Native or Introduced Grasses	none
46 Urban	none

**Bat species known to use each Texas Parks & Wildlife association were modeled as occurring in matched Holdridge vegetation types. (Holdridge associations 21–23, 37, 40 were not matched to vegetation currently occurring in Texas.) Adapted from Cameron & Scheel 1993.*