What parts of the US mainland are climatically suitable for invasive alien pythons spreading from Everglades National Park?

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Abstract

The Burmese Python (*Python molurus bivittatus*) is now well established in southern Florida and spreading northward. The factors likely to limit this spread are unknown, but presumably include climate or are correlated with climate. We compiled monthly rainfall and temperature statistics from 149 stations located near the edge of the python's native range in Asia (Pakistan east to China and south to Indonesia). The southern and eastern native range limits extend to saltwater, leaving unresolved the species' climatic tolerances in those areas. The northern and western limits are associated with cold and aridity respectively. We plotted mean monthly rainfall against mean monthly temperature for the 149 native range weather stations to identify the climate conditions inhabited by pythons in their native range, and mapped areas of the coterminous United States with the same climate today and projected for the year 2100. We accounted for both dry-season aestivation and winter hibernation (under two scenarios of hibernation duration). The potential distribution was relatively insensitive to choice of scenario for hibernation duration. US areas climatically-matched at present ranged up the coasts and across the south from Delaware to Oregon, and included most of California, Texas, Oklahoma, Arkansas, Louisiana, Mississippi, Alabama, Florida, Georgia, and South and North Carolina. By the year 2100, projected areas of potential suitable climate extend northward beyond the current limit to include parts of the states of Washington, Colorado, Illinois, Indiana, Ohio, West Virginia, Pennsylvania, New Jersey, and New York. Thus a substantial portion of the mainland US is potentially vulnerable to this ostensibly tropical invader.

Key words: *Python molurus*, Burmese Python, geographic range, invasive species, Florida Everglades, climate matching, temperature, precipitation

Introduction

Invasive alien species are proving to be a major challenge for the conservation of biodiversity (Wilcove et al. 1998). Invasive alien reptiles have received less attention than other vertebrate taxa (Lever 2003), although the Brown Treesnake's (*Boiga irregularis*) invasion of Guam has been widely reported (Savidge 1987; Rodda et al. 1999). The recent irruption of Burmese Pythons in Florida's Everglades National Park has brought concern about invasive snakes to the US mainland (Snow et al. 2007, in press).

The Burmese Python is a questionable subspecies of the Indian Python, *Python molurus* (McDiarmid et al. 1999). The Everglades population of Indian Pythons is believed to have derived from unwanted pets released in the park (Snow et al. 2007). The likely proximate impetus for their disposal is the snake's unmanageably large adult size (up to 7-8 m, 90 kg) and voracious appetite, which challenges even advanced herpetoculturists to supply the necessary food and space (Walls 1998).

The huge maximum size of the Indian Python is also a concern with regard to invasiveness, both due to the broad spectrum of predator sizes represented and the possibility that resident prey species may not have evolved defenses against a novel-sized predator (Ehrlich 1989, Veltman et al. 1996, Allen 2006). In their native range, hatchlings eat a variety of small vertebrates, but large adults specialize in eating large mammals (Wall 1912, 1921). The species' range of body sizes allows pythons at some life stage to eat most terrestrial endothermic vertebrate species found in Florida, and animals ranging in size from house wrens to white-tailed deer have already been removed from the stomachs of pythons captured in Florida (Snow et al. in press). Large Indian Pythons are also capable of killing humans, including full-size adults (Chiszar et al. 1993). The aggregate national burden of these ecological and human health risks is of great interest to policymakers; yet it is difficult to assess, and depends at least in part on how geographically extensive is the python's ultimate distribution (Bomford et al. 2005).

In Florida there are 31 vertebrates listed as threatened or endangered under the US Endangered Species Act that are of a size and habit that may be vulnerable to consumption by Indian Pythons, and an additional 41 species or subspecies that are biologically rare (< 100 occurrences or <10,000 individuals: Florida Natural Areas Inventory 2007) but not listed by the federal government. But this accounting assumes that pythons spread throughout the entire state; is this assumption warranted?

In the popular imagination, pythons are considered to be creatures of the tropical jungle, as typified by the character of Kaa, the python in Disney's adaptation of Kipling's *The Jungle Book*. Even among biologists, there is a common assumption that invasive Indian Pythons will be restricted to southern Florida. This assumption, however, is belied by an examination of the Indian Python's native range, which extends well into more temperate climate zones in China and the Himalayas.

What is known about the factors that delimit the python's range in China and the Himalayas? Unfortunately, little is known about the factors that delimit any part of the python's range. Indeed, understanding the factors that control a species' range limits is one of the fundamental challenges of ecology (Krebs 1978). It is especially difficult for a species whose population biology is as poorly researched as is that of the Indian Python. On a demographic level, range limits must represent the set of geographic points at which recruitment and immigration just fail to offset mortality and emigration. Recruitment and population movements (emigration/immigration) in snakes are highly sensitive to energetic factors such as prey availability (Seigel et al. 1987). Physiological tolerances may be involved in some areas, but demographic or energetic limitations may be more constraining than physiology. Unfortunately, relevant demographic, energetic, or physiological values are unknown for any place in the python's range. As a proxy for such factors, most ecologists look at broad regional gradients such as climate, as climate often exhibits a rough correlation with range limits.

Inspection of the western distributional limit of the Indian Python reveals a striking irregularity (Fig. 1). The western edge of the species' range is an erratic loop that excludes most of the Thar or Great Indian Desert but includes riparian areas along the upper and lower reaches of the Indus River system. It does not include the extremely arid areas away from the rivers or in most of Baluchistan or Western Pakistan. From this we infer that aridity is likely to be a limiting condition in this part of the range.

The southern and eastern limits mostly follow the edge of the Asian continent (Fig. 1). Presumably the python could tolerate more extreme environments than those inhabited, but we have no way of inferring what those conditions would be.

The northern limit of the python's range (Fig. 1) lies in the foothills (~2400 m) of the Himalayan mountains in Pakistan, India, Nepal, and Myanmar, and is bounded by a combination of high altitude and high latitude (e.g., Sichuan Province). The range limit east of Sichuan swings southward to exclude most or all of Hubei and Hunan provinces, a low elevation area that experiences bitterly cold winters. A reasonable first approximation would be that the northern range limit is associated with cold temperatures, or some feature such as energetic limits (e.g., prey availability) correlated with cold temperature.

Sustaining a python population under temperate conditions likely requires winter hibernation, and the phenology of annual activity reported for northern Pakistan (Minton 1966) indicates that the Indian Python hibernates for up to at least four months (it may hibernate for longer in other areas). We do not know what factors control hibernation initiation or duration, however (Wall 1912, 1921; Bhupathy and Vijayan 1989). Muscle physiology may limit python activity to above a certain temperature threshold for locomotor activity, or limited energy intake during active months could fail to sustain a long hibernation. Well-fed snakes, especially large individuals, generally can physiologically tolerate multi-year fasts (McArthur 1922), but the ecological success of a population may be limited by energetic factors or physiological factors short of immobility or lethal starvation. Furthermore, the interpretation of physiological data on thermal tolerance is complicated by the absence of appropriate information on available environmental conditions. We can extract the air temperatures to which a specific venue is subjected, but we cannot easily know the microclimates experienced by a snake at that venue. Put another way, knowing the extreme low temperature in a given month may not be important if the pythons retreat to underground burrows at the time of day when the low temperatures prevail. Obtaining physiological, environmental, and behavioral data sufficient for parsing the evolutionary integration of energetic and physiological factors for a single site in the native range would be experimentally challenging and would require a comprehensive understanding of paleo-climates and the evolution of python hibernation behavior. Such information is likely to remain unavailable for some time; meanwhile, insight into the potential US distribution is needed immediately to inform management of this rapidly expanding invader.

Environmental niche models (Nix 1986, Stockwell and Peters 1999, Scott et al. 2002) generally attempt to identify a unitary set of environmental conditions that distinguish occupied from unoccupied areas. Occupied habitats range from thorn-scrub desert, chapparal, and grassland steppes to hot/humid evergreen tropical forest, montane dry forest, and temperate deciduous forest (Wall1921, Minton 1966, Groombridge and Luxmoore 1991, Schleich and Kästle 2002). Unfortunately, habitat mapping is unavailable for major portions of the snake's native range, and the proximate factors associated with a particular Asian habitat (e.g., timing of monsoon arrival) may not be applicable to New World localities. Based on the boundaries of the native range distribution, we believe that no single suite of factors limit python distribution throughout its range. Furthermore, only a few locality records of sufficient resolution are available in association with detailed environmental correlates (slope, elevation, temperature, etc.) to build credible unitary niche models. Thus the opportunities for traditional niche modeling are limited in this case, and may not be appropriate (O'Connor 2002, Guisan et al. 2006, Broennimann et al. 2007, Rodda et al., in press). Instead, we consider a range of seasonal temperature and rainfall conditions and hibernation behavior that are plausible based on observable climate envelopes from the python's native range. Our method is similar to the CLIMEX modeling technique that has been used extensively to predict the spread of non-native pest and weed species using climate data from their native range and species-specific life history parameters (Sutherst and Maywald 1985). We inspect the local climate records for evidence of hibernation and aestivation durations, and match those climate conditions to localities with equivalent climates in the US.

Methods

We used published sources to infer the native range of *Python molurus* (Appendix). We used exact specimen locations whenever available, and more general regional information when unavoidable, paying particular attention to records from high elevations and high latitudes. As we were focused on the climatic extremes tolerated by the species, we compiled only those locality records within 3 lat/long degrees of the periphery of the species' range (spot checking of more interior localities indicated that inclusion of interior localities failed to expand the observed climate envelope).

"Presence" localities were matched to the geographically closest choice from among the 85,000 weather stations reported in the World Climate (2007) data set, paying particular attention to ensure an elevation match (where known). When possible, we used individual weather stations that reported both mean monthly rainfall and mean monthly temperature, but in a few cases combined records from nearby stations to obtain both climate data types. The World Climate stations are grouped into lat/long cells of 1 degree; we matched these to locality records in the same cell whenever possible, but for a few important localities could find matching weather records only for an adjacent cell (only stations with similar elevations were considered). We were able to obtain a few useful climate records for locations hosting Indian Pythons in Nepal from Schleich and

Kästle (2002). To analyze rainfall on a logarithmic scale and include weather stations that reported zero rainfall during particular months, we coded zero rainfall means as 0.01 mm/mo. We were able to match 149 localities with appropriate climate data from 11 countries (Bangladesh 8, Cambodia 3, China 43, India 34, Indonesia 14, Myanmar 8, Nepal 6, Pakistan 10, Sri Lanka 8, Thailand 9 and Vietnam 6).

We plotted each of the 149 climate records as 12-sided polygons, each vertex representing the mean conditions for one month of the year. We anticipated that the aggregate climate space occupied by the 149 polygons would be reasonably well defined by tolerance of high heat and maximal rainfall, but would have irregular excursions into climate spaces of extreme cold and aridity, representing periods of hibernation and aestivation respectively.

By progressively flagging the first, second, and third months of greatest aridity against the graphical background of the 149 climate polygons, we observed that only the first and second-most arid months were largely confined to sparsely-occupied climate space. From this we inferred that *Python molurus* generally avoids extreme aridity but is probably capable of up to 2 months of aestivation in these habitats. We attempted a similar analysis for hibernation periods of 2-5 months, but did not observe a clear distinction between sparsely-occupied and routinely occupied climate space at the cold limit of the species' climate space. In light of the four month hibernation period reported for Pakistan (Minton 1966), we evaluated alternate hypotheses of 3 (Clim3) or 4 (Clim4) months of hibernation.

For each hibernation hypothesis we fit the closest convex polygon that included all points believed to represent climatic conditions experienced by active pythons (i.e., excluding those points deemed hibernation or aestivation), and checked these climate hypotheses against field observations reported in the literature or by personal communication from appropriate experts. We also applied our climate envelope hypotheses to current world climate data layers for monthly temperature and precipitation modeled from weather station data from around the world to a 1km resolution (Hijmans et al. 2005) to verify if all occupied native range sites were identified as suitable.

Finally, we applied the climate envelope defined by the 149 climate polygons to the current climate and future climate scenarios for the US. We obtained average monthly precipitation (cm) and average monthly temperature (ºC) data from the on-line Daymet database for the United States (http://www.daymet.org; Thorton et al 1997). Thorton et al (1997) used daily observations from over 6000 stations across the United States collected from 1980 to 1997 to create the surfaces at a 1 km^2 resolution. Our future climate scenario consisted of climate layers derived from models of climatic response to greenhouse gases developed by the National Center for Atmospheric Research (NCAR), CCM3, for 2100 (Govindasamy et al. 2003). These predictions for 2100 included average monthly precipitation and average monthly temperature.

The equations defining the climate space of the convex polygon occupied by the 149 climate polygons were implemented using Visual Basic for Applications with ESRI's ArcGIS 9.0 ArcObjects to produce the US map of climate suitability for the python. These were done using the same code for both the Clim3 and Clim4 climate scenarios paired with each of the climate scenarios. The final maps were produced by comparing the one generated using the Clim3 equations to that using the Clim4 equations using the

Raster Calculator in ArcGIS to determine areas where the hibernation scenarios matched and differed.

Results

Our assessment of the native range of *Python molurus* is shown in Fig. 1.

The 149 climate polygons from the python's native range covered a wide range of tropical, sub-tropical, and temperate climates (Fig. 2). Indian Pythons live in places that have monthly mean temperatures of 2 - 37 ºC. Under moderate conditions of temperature, pythons appear able to routinely tolerate localities with monthly mean rainfall of 1-2000 mm/mo. Pythons live in many places with up to two consecutive months of zero recorded rainfall, but the pattern of occupied climate spaces suggests that they rarely if ever populate places where mean rainfall is less than that indicated by the octagon in Fig. 2 for more than 2 months. Similarly, they live in places with months of mean temperature as low as 2 ºC, but probably hibernate at such low temperatures. If they can hibernate for no more than 3 months (Clim3), they must be active under conditions corresponding to a mean monthly temperature of >7 ºC, whereas if they can hibernate for 4 months (Clim4), they must be active under conditions corresponding to a mean monthly temperature of > 9 ºC. Thus Clim4 does not indicate a greater cold tolerance, but activity at a higher mean temperature combined with a tolerance for a longer period of inactivity; Clim3 thus combines a slightly greater cold tolerance with ability to tolerate a slightly shorter period of inactivity.

We were unable to find published records associating python activity with low environmental temperatures, but Max Nickerson (Florida Museum of Natural History) reported to us that he observed pythons active in northern India at 10 C, suggesting that either of our hibernation hypotheses would be consistent with his observation. Bhupathy and Vijayan (1989) interpreted a paucity of summer python sightings at their study area to suggest aestivation, but they were unable to verify this or estimate duration of potential aestivation.

The map displaying the association between Clim3 and Clim4 projected to a current global weather model (Fig. 3) indicated that our climate hypotheses correspond to virtually all of the native range sites except for a small area in extreme western India, and peninsular Malaysia south of the Isthmus of Kra. On the west, areas outside of the occupied native range were primarily the Great Indian Desert, a strip to the west of occupied range in western Pakistan and parts of coastal eastern Iran. Climatically suitable range was also identified north of occupied range in eastern China.

The identification of North American localities with such climates indicated a broad swath of suitable climate across the southern tier of states (Fig. 4). Only a small area of the Colorado Desert in southern California and a small area along the coast in Santa Barbara County were found to be too arid by both scenarios (and only an additional ~180 km^2 were deemed too arid by Clim4). The majority of the 48 states was judged too cold under one or both hibernation hypotheses. Suitable areas included most of 11 states (West to East): California, Texas, Oklahoma, Arkansas, Louisiana, Mississippi, Alabama, Georgia, Florida, and South and North Carolina. Parts of 12 states had suitable climate (W to E): Oregon, Nevada, Utah, Arizona, New Mexico, Kansas, Missouri, Kentucky, Tennessee, Virginia, Maryland, and Delaware. Although the difference between the two hibernation hypotheses was relatively insignificant on a continental scale, potential boundary shifts of > 100 km occur in northern Texas and Oklahoma, southern Kansas, Tennessee and central Virginia (a total of about 281,583 km^2 distinguishes the areas deemed suitable under the two hibernation hypotheses). Based on the climate space identified (Fig. 2), and the mapped presence of suitable climate along the Mexico-U.S. border (Fig. 4), the climate would appear to be suitable for pythons well into Mexico and potentially much of the Neotropics.

As expected, the climate model for the year 2100 projected additional suitable area to the north of the current limit (Fig. 5). Additional states partially included under at least one scenario were: Washington, Colorado, Illinois, Indiana, Ohio, West Virginia, Pennsylvania, New Jersey, and New York. The differences between the Clim3 and Clim4 projections for the year 2100 were more extensive than with current climate conditions, especially in the Midwest.

Discussion

The native range limits that we identified (Fig. 1) correspond closely to those identified by Groombridge and Luxmoore (1991) except in China, for which Groombridge and Luxmoore (1991) indicated a near absence of information. Our alignment in China corresponds closely to the map produced by Ji and Wen (2001) except that we exclude the Tibetan Plateau. Ji and Wen (2001) gave no justification for inclusion of the Tibetan Plateau; thus we can only speculate that pythons may reside there very locally within deep river valleys, as the prevailing climate on the plateau would appear to be much too cold and we know of no specific locality records either within the plateau or elsewhere at such high elevations.

The projection of our climate hypotheses to the python's native range (Fig. 3) was encouraging in that virtually all of the occupied native range was shown as suitable. The exclusion in western India may have some relationship to the absence of pythons from the Great Indian Desert just north of this exclusion. The Hijmans et al. (2005) weather record set used for this projection has very little empirical data for the Great Indian Desert (we located none in the WorldClimate.com data set), and the slight geographic mismatch may be attributable to the lack of appropriate empirical climate records.

Our native range map (Fig. 1) shows an absence of *P. molurus* south of the Isthmus of Kra in peninsular Malaysia, but the entire peninsula was projected to have suitable climate using our climate hypotheses (Fig. 2) in relation to the Hijmans et al. weather record set (Fig. 3). Indian Pythons are also absent from Borneo, Sumatra, and most of the Lesser Sundas and Maluku Islands, but occur on Java, Sumbawa, and the southwestern arm of Sulawesi; all of these islands were projected to have climate suitable for the species. Two hypotheses are reported in the literature to account for this disjunct distribution (Saint-Girons 1972, Minton and Minton 1973, Murphy and Henderson 1997, Walls 1998). The first is that the Indian Python's range ends naturally at the Isthmus of Kra and the disjunct populations on Java, Sumbawa, and Sulawesi represent prehistoric human introductions (prehistoric in the sense that no written record exists of human-aided transportation of the snake or of a time prior to the python's residency on those three islands). The second hypothesis is that of localized competitive displacement by *Python reticulatus*, manifest more readily on islands or peninsulas, for which recolonization is less likely. It is notable in this regard that male *P. reticulatus* bite each other savagely when in competition for mates, and may defend space (Lederer 1944, Barker and Barker

1997, Auliya 2006), whereas male *P. molurus* exhibit non-damaging scramble competition for mates and have widely overlapping activity ranges. The climate projection we present (Fig. 3) is consistent with the latter hypothesis, but does not constitute a strong test.

In keeping with the precautionary principle, we bounded our climate hypotheses (Fig. 2) to include all documented suitable climate space, rather than attempting to identify the rainfall and temperature thresholds that best discriminate between occupied and unoccupied native range. Accordingly, we expected and observed some over-prediction in the area of western Pakistan and eastern China. The amount of over-prediction is somewhat difficult to quantify because historic range contractions in both of these areas may have excluded habitat that is otherwise suitable. Minton (1966) and Groombridge and Luxmoore (1991) observe that pythons were reported to be more widely distributed to the north and west in earlier historic times, but human persecution is believed responsible for range contraction.

Although the python resides naturally in tropical sites straddling the equator, the more temperate parts of Indian Python native range correspond climatically to many southern and southwestern US states (Fig. 4). According to 2000 census figures, about 120 million Americans live in counties having climate similar to that found in the native range of the python. Many more Americans live in areas that could be colonized by Indian Pythons if the global climate warms as predicted by many models (Fig. 5).

Will the python extend its range as far as suggested by this climate match? As we have not identified the ecological phenomena limiting the natural distribution of the snake, it is not yet possible to determine the equivalent North American boundaries. For example, Rodda et al. (1999) obtained evidence suggesting that ecological success of the invasive Brown Treesnake was limited primarily by food availability. Although climate is likely to be correlated with snake food availability, the correspondence may be only general, enabling climate to both under-predict and over-predict an invasive species' eventual distribution. Furthermore, the gene pool of the North American population of *P. molurus* may include only a small subset of the genetic variability found in the native range; the invader population may not adapt to the full range of ecological conditions present in climatically-suitable parts of North America.

African pythons (*Python natalensis*) are believed to be climate-limited at the temperate edge of their African range by virtue of inhospitable incubation conditions rather than survival difficulties (Alexander 2007). If this phenomenon applies to Indian Pythons as suggested by Vinegar *et al.* (1970), the pythons in North America might be able to occupy but not sustain populations in sites north of areas indicated by their species' climate envelope. Alexander (2007) further reported that brooding female *Python natalensis* do not appear capable of warming their eggs by shivering thermogenesis, whereas this capability is well documented in Indian Pythons (Van Mierop and Barnard 1978). Thus, there is reason to think that the differential climate limit for python reproduction and survival might apply only to species, such as *P. molurus*, exhibiting shivering thermogenesis.

The method we used for identifying the climate envelope for *Python molurus* has not been widely used by invasive species climate matching models in recent years. Some observers favor automated regression fitting models such as GARP (Genetic Algorithm for Ruleset Prediction: Stockwell and Peters 1999) or BIOCLIM (Elith *et al.* 2006).

These methods have merit, especially for invertebrate or plant species for which physiological limits are likely to be well documented and fairly inflexible. However, we chose not to use these for the Indian Python for three reasons. We wished to avoid fishing for climatic correlates with insufficient statistical protections against over parameterization. Furthermore, much of the perimeter of the python's native range is delimited by saltwater, and therefore uninformative as to the conditions potentially tolerated. The automated climate matching programs tend to give equal weight to all occupied climate space, including uninformative localities. Finally, the automated climate matching programs work best if the environmental conditions limiting a species' distribution are consistent across much of the native range perimeter; our method better accommodates a diversity of limiting conditions.

The rapid spread of the python northward from the Everglades, and the large potential distribution of the python in the New World are two factors adding urgency to management efforts for this invader. The state of Florida is planning control activities to stop the spread of Indian Pythons south of Lake Okeechobee (S. Hardin, Florida Game and Fish Comm. pers. comm. 2007). Stopping the spread in the relatively narrow confines of the Florida peninsula would appear to be easier than controlling a much wider invasion front that may occur if the python spreads beyond peninsular Florida, as this work suggests is climatically possible. Nonetheless, there appear to be no precedents for containing an expanding continental snake population. The large potential range of the python in the New World suggests that early control may be a preferred option. Our results also indicate that additional populations of Indian Pythons could become established as a result of releases across a wide swath of the United States, and continued vigilance will be vital to early identification and eradication of extralimital infestations. Release of unwanted pets should be avoided under all circumstances, and release of *P. molurus* in the areas flagged as "suitable" in this study constitutes the highest risk of fostering a new locus of infestation.

Acknowledgments

We thank RW Snow for sage counsel and access to unpublished data on pythons in Florida, and D Kimball for encouraging us to document the role of global climate change in advancing the habitable boundaries. Support for this work was provided by US Geological Survey and the US Department of the Interior's Office of Insular Affairs. LR Bonewell, BM Lardner, RJ Rondeau, and AS Wiewel suggested improvements to the manuscript.

Appendix. Sources used to infer the geographic range of *Python molurus*

Campden-Main 1970

Caras 1975

Chan-ard et al. 1999

Cox et al. 1998

Daniel 2002

Das 1994, 1996, 2002a, 2002b

Das and De Silva 2005

de Haas 1950

de Rooij 1917

Deuve 1970

Deyang 1986

Groombridge and Luxmoore 1991

Ji and Wen 2001

Kabisch 2002

Karsen et al. 1986

Lang and Vogel 2005

Manthey and Grossmann 1997

Maslin 1950

McDiarmid et al. 1999

McKay 2006

Mertens 1930

Minton 1962, 1966

Minton and Minton 1973

Murphy and Henderson 1997

Pope 1935, 1961

Smith 1943

Swan and Leviton 1962

Vinegar et al. 1970

Wall 1912, 1921

Wall and Evans 1900

Welch 1988, 1994

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Captions to figures

Figure 1. Native range limits (solid black line) used in this analysis, plus place names mentioned in text. See Methods and Appendix for additional information.

Figure 2. Climate space under two hibernation duration hypotheses. Clim3 allows a three month hibernation; Clim4 a four month hibernation.

Figure 3. Projection of the Clim3 and Clim4 climate hypotheses to south and southeast Asia, using the global climate model prepared by Hijmans et al. (2005).

Figure 4. Areas of the continental United States within the climate envelopes represented in Figure 2 based on DAYMET climate layers for the United States.

Figure 5. Areas of the continental United States within the climate envelopes represented in Figure 2 based on projected 2100 climate (NCAR CCM3 model).