5-6-2011

The Fate of Alpine Species in the Face of Climate Change: A Biogeographic Perspective

Madaline Cochrane
Macalester College

Follow this and additional works at: http://digitalcommons.macalester.edu/biogeography

The Fate of Alpine Species in the Face of Climate Change: A Biogeographic Perspective

Madaline Cochrane

ABSTRACT

Will global climate change affect the spatial distribution and abundance of biodiversity along mountains equally? The elevational gradients inherent as one moves up a mountain slope help define the many biological patterns that emerge as key indicators for species richness in an era of rising global temperatures. When global temperatures rise, the microclimates found along different elevational ranges on mountains also fluctuate. As abiotic characteristics such as daily air temperature, daily precipitation, and annual snowmelt change overtime, so will the biotic communities on a mountain. Some species may be able to adapt to their new environments, while other may have the capacity to shift their ranges upward. However, the biological realities facing mountain species vary given the elevational and life history characteristics of each individual species. This review paper summarizes many of the major biogeographical patterns that have been observed to occur on elevational gradients as a result of global warming. This is by no means an all-inclusive report on the state of scientific knowledge in this important field, but instead a discussion of the varied ecological realities facing biota along mountains throughout the world.

INTRODUCTION

The geographic template, for which all life on Earth relies on, has become increasingly less stable in the last half century. As anthropogenic greenhouse gas concentrations have grown exponentially in Earth's atmosphere, the major wind, precipitation, and temperature gradients of the world have begun to change. Across the globe the biotic world is now in a position in which alterations are inevitable, especially among the biota that resides on mountains. If climate change acts as expected and increases global sea surface temperatures, the cascading effects related but not limited to shrinking glaciers, altered precipitation patterns, and disruption of wind circulation, on alpine biota could be immense (IPCC, 2007). The role of biogeography in predicting the fate for thousands of alpine species cannot be understated. Using climatic and biological data from the last century, as well as paleoclimatic and paleobiological data from both glacial and interglacial periods in our geological history, we can begin to understand and model the future for mountain species. The study of biogeography encompasses how species interact amongst their abiotic and biotic environments across spatial scales. Those very interactions will define the fate of mountaintop species.

Table 1. Major themes included in the study of the biogeography of mountain species in an era of global climate change, including subthemes and literature sources for each subtopic.

Theme	Source
Elevation & Abiotic	
Climate induced altitudinal range shifts & upslope species displacement	Davis & Botkin, 1985; Prentice, 1986; Huntely, 1990; Prentice et al., 1991; *Hill et al., 2002; Kullman, 2002;* Song, Zhou, & Ouyang, 2005; Colwell et al., 2008; Raxworthy *et al.*, 2008
Running out of a range & mountaintop endemic extinctions	Sekercioglu et al., 2008; Xu *et al.*, 2009
Climatic induced tree line shift	Song, Zhou, & Ouyang, 2005; Truong, Palme, & Felber, 2007; Xu et al., 2009
Climatic induced orographic cloud base shift & biotic implications	Pounds, Fogden, Campbell, 1999; Still, Foster, Schneider, 1999
Taxonomic Diversity Gradient	
Variability of habitat hetereogeneity in an era of melting snowpacks	Brown, Hannah, & Milner, 2007
Elevation & Phenology	
Disjunction of low and high elevational phenologies	Inouye *et al.*, 2000; Xu et al., 2009
Disjunction of pest-host phenologies	Bylund, 1999; Watt & MacFarlane, 2002; Logan, 2003
Dispersal of Diseases	
Facilitation of spread of infectious diseases	Pounds *et al.*, 2006; Lips et al., 2008
Dispersal and Genetic Diversity	
Mountaintop refugia & limitations to gene flow	MacArthur & Wilson, 1967; Brown, 1971; Orloci, 1994; Gottfried et al., 1999; Floyd, Vuren, & May, 2005; Ditto & Frey, 2007; Truong, Palme, & Felber, 2007

ELEVATION AND ABIOTIC

As global temperatures increase, the microclimates of mountains are also changing. We should expect to see warmer temperatures at each altitudinal range along mountains. As a result, biota adapted to the envelope of temperatures, precipitation, and sunlight at a specific range of elevations, will have to expand their range upwards or radically adapt to new abiotic environments if they intend to survive. This classic biological fingerprint of global warming is called upslope species displacement (Raxworthy *et al.*, 2008).

In an example of species movement across space, a study on the highest massif in Madagascar found that herpetological species experienced an upslope displacement of 17-74 meters between the years of 1993 and 2003. This upward

range expansion was observed in conjunction with a 1.7°C temperature increase over that time span (Raxworthy *et al.*, 2008). In other studies related to global climate change, scientists have predicted a 400-600 meter increase in altitudinal range margins of vegetation zones over the next several decades (Hill *et al.*, 2002; Kullman, 2002). The biological realities of such shifts are immense. First, as species move up in elevation they come into contact with the biota already living along that altitudinal gradient. The displacement of these native species is a climate-induced consequence that biota face on mountains around the world. Competition for resources will increase and once ecologically adapted species must be able to keep pace with the rapidly changing abiotic environment. Of major concern are endemic species only found on mountaintops. These unique organisms, once extirpated, will be gone forever. This problem is particularly enhanced in montane environments as endemism is positively correlated with elevation. As a result the species found at the top of mountains, some of which are already the most vulnerable to climate change, are also those often found no where else on Earth.

The remote and unforgiving environments such as those found on the highest peaks in the world—the Himalayas—tend to be more susceptible to climate change than the environments and their biota found at lower elevations. The size of the ecological niches of species at high elevations can only decline in the future as these organisms face the challenges of declining niche availability. Many species currently situated at the top of mountain will have no place to migrate upwards and away from rising temperatures, vegetative, and animal range shifts (Xu *et al.*, 2009). Certainly of major biogeographical concern for the conservation of species diversity in the near future is the reality that mountains can't possibly be high enough to offer escape routes to all species as upward shifts in taxa persist.

The primary concern for conservationists interested in mountaintop displacement is extinction. In a study of landbird species all across the world, researchers found that a 2.8°C increase in global sea surface temperatures has the potential to cause 400-550 landbird species extinctions, hundreds of which

4

reside on mountaintops (Sekercioglu *et al.*, 2008). The limitations imposed on species and their ranges through elevation include climatic, ecological, and physiological realities. Topographic isolation and harsh abiotic environments often found on mountaintops correspond to high levels of adaptation and isolation (Xu *et al.*, 2009). The species once able to survive on mountaintops are subject to an ecological trap as the specializations that allowed them to survive in such unforgiving habitats now leave them unable to adapt to their changing environments or out-compete other generalist species moving into their homes. For example, as mountaintops are colder than lowland elevations, species living in alpine environments typically require higher metabolisms in order to gain enough food to maintain stable body temperatures throughout the year and during the night when ambient temperatures can become frigid. These specific adaptations for the current abiotic environments will prove problematic; as temperatures increase, their ranges decrease in size, and the availability of food declines with rising levels of biotic competition. Consequently, the very adaptations that have allowed these species to become specialized in their unique, alpine environments leave them less likely to out-compete generalist species better adapted to warmer and homogenized surroundings. These unfortunate realities should be taken into consideration through potential conservation measures. However, 67% of birds predicted to become extinct in the previous model are not considered threatened today (Sekercioglu *et al.*, 2008). Indeed it is hard to remain optimistic when even the best conservation efforts cannot possibly save species as their native environments disappear along with them.

In other biogeographic analyses of species movement, a recent study in Costa Rica found that altitudinal range shifts appear to be much stronger than latitudinal range shifts. This proved particularly dominant within the tropics in which a shallow latitudinal temperature gradient exists (Colwell *et al.*, 2008). These range shift patterns manifest themselves through lowland biotic attrition near the base of mountains, as species moving upwards are not replaced with downward shifts in species distributions. At mid-elevations along tropical

mountain we find that a new concern emerges. Here species are projected to experience gaps between current and projected elevational ranges (Colwell *et al.*, 2008). These range-shift gaps prove ecologically problematic when species, often ill-adapted for upwards migration, can't disperse across large distances in order to remain within the physical gradients they are adapted to survive in. Upslope shifts in climatic isotherms such as rising temperature gradients could spell a lot of trouble for taxas at mid-elevations who do not have the ability to disperse and cannot compete with new species moving into their elevational life zones. In addition, organisms capable of dispersal or migration upwards must still become established within their new, unstable environments. Surviving upward migration and thus moving across space doesn't ensure a species survival. Species must also become established in new environments with new ecosystem structures and species diversity, Whether biotic attrition, range-shift gaps, or upslope displacement, the biota of mountains will need to adapt quickly and out-compete new competitors in order to survive in rapidly shifting environments.

In the future we can expect life zone contraction and expansion, in addition to vegetation distribution shifts on mountains. Using data related to the distribution of vegetation types on the Tibetan Plateau from the early Holocene, when temperatures were elevated just like they are becoming today, researchers can predict that forest, shrub steppe, alpine steppe, and alpine meadow will grow in size while desert vegetation will diminish (Song, Zhou, & Ouyang, 2005). In fact many results from paleobotanical studies have confirmed climate-induced changes in ecosystem diversity (Davis & Botkin, 1985; Prentice, 1986; Huntley, 1990; Prentice *et al.*, 1991). While regionally we will expect varying shifts in vegetation distributions depending on biota already existing, a global trend that has been observed are rising tree lines in temperate ecosystems (Song, Zhou, & Ouyang, 2005; Truong, Palme, & Felber, 2007; Xu *et al.*, 2009). As temperatures increase at higher elevations, trees are now able to survive at higher elevations as a result of lessening environmental constraints at high elevations, including shrinking year-round snow packs. In the Eastern Himalayas researchers estimate that tree-line has crept upwards by 110 meters over the past century (Xu *et al.*,

2009). Montane trees, often dwarfish in size, are some of the only noticeable plants able to survive in such windy, cool environments found at high elevations along temperate mountaintops. These trees, and those like them all across the globe, are able to shift up in elevation despite abiotically-restrictive environments that prevent other plants from becoming established in these barren settings.

Temperature is not the only abiotic characteristic that influences the biotic. In fact increased sea surface temperatures have many indirect effects on other abiotic characteristics that also alter elevational patterns of biota on mountains. As an example, using data from the Last Glacial Maximum to predict models for future scenarios of increased carbon dioxide concentrations, scientists expect upward altitudinal shifts in tropical cloud forest ecosystems, based largely on the fact that clouds, the basis for life in such ecosystems, are also moving upwards. This lifting-cloud-base hypothesis suggests that atmospheric warming has resulted in an increase in the altitudinal base of the orographic cloud bank. These orographic clouds form as wet air from the Caribbean is forced up over the tops of mountains such as the Tilaran Range of Costa Rica (Pounds, Fogden, Campbell, 1999).

Due to an enhanced hydrological cycle, as a result of rising global temperatures, scientists have identified a shift from a dry to a moist adiabatic lapse rate at low latitudes along the Central American isthmus (Still, Foster, Schneider, 1999). This change to a moist adiabatic lapse rate, decreases the rate at which air particles cool as they rise up steep slopes such as the Tilaran Mountains. This pattern has shifted the average elevation of the orographic cloud base essential to life in cloud forests. These environments are particularly vulnerable to changes in precipitation and cloud cover as the clouds themselves provide a misty-environment essential to epiphytic plants, as well as many populations of animals including amphibians reliant on moist environments. Indeed, recent studies have linked amphibian, reptilian, and bird population crashes from within the cloud forests of the Neotropics in the late 1980s to global temperature increases (Pounds, Fogden, Campbell, 1999). Reduced cloud contact and increased evapo-transpiration have proven insurmountable

obstacles for species adapted for humid environments. Altered elevational distributions of clouds and precipitation are only one example of how climate change can affect our physical environment in predictable fashions across the globe. The shrinking of our alpine glaciers is another example of the enormity of the potential biotic whiplash that will be encompassed as a result of cascading effects related to rising sea surface temperatures.

TAXONOMIC DIVERSITY GRADIENT

Global warming will have global, regional, and site-specific effects on species diversity. In one study completed in the French Pyrenees, researchers suggest that shrinking glaciers and snowpack will act to homogenize habitat heterogeneity over the entire region. The habitat in this area is particularly diverse as a result of both spatial and temporal variability in the amount of glacial snowmelt effecting different locations along the Pyrenees (Brown, Hannah, & Milner, 2007). Future meltwater reductions, due to global warming induced shrinking glaciers and snowpack, will cause diversity at the site of each stream, presently fed by meltwaters, to increase on average. The researchers found that macroinvertebrates survive better with the homogenized warmer water temperatures, lower suspended sediment concentration, higher pH, and higher electrical conductivity, all associated abiotic characteristics of meltwater reductions. Yet, diversity between sites was found to be reduced as habitat heterogeneity was slowly eliminated and endemic species living in specialized stream environments, and thus not well-adapted to warmer and decreased quantities of meltwater, went extinct. As a result, the researchers predict diversity across the region to decrease over time as global warming reduces alpine snowfall accumulation. This reduction in annual snowfall will continue to reduce the quantity of meltwater until it is eliminated all together (Brown, Hannah, & Milner, 2007). The fate of species richness across a range of taxa and not just constrained to alpine, stream environments is in flux. Biological mountain hotspots rich in endemism might prove the most susceptible to homogenization as climate change commences.

ELEVATION AND PHENOLOGY

Biota living at high elevations and high latitudes often exhibit distinct seasonal variability. The seasonal patterns associated with bud-out in plants or emergence of a mammalian species from hibernation are often on strict phonological life cycles. The timing for such changes corresponds to increased solar radiation found during the summer months at higher latitudes. This seasonal fluctuation in solar radiation results from the tilt of Earth on its axis as it rotates around the sun. These seasonal fluctuations in temperature and precipitation help to melt winter snowpacks and allow plants to grow at locations, unlike the tropics, where growth is confined to long-periods of photosynthesis found during the summer months. Both plants and animals take advantage of increased energy resources to reproduce and garner enough reserves for the colder and darker winters. However, climate change has the potential to disrupt the physical cues that control when plants and animals emerge from winter dormancy to take advantage of summer resources. Of particular concern are recent studies that indicate how climate change affects the phenology of species in each elevational range differently.

In fact, at a high altitude study site within the Rocky Mountains researchers have noticed a disjunction between the phenology of low and high altitude plants and animals (Inouye *et al.*, 2000). The calendar date for the beginning of the growing season at their high altitude study site, hasn't changed significantly over the past 25 years, most likely as a result of increased winter precipitation. While higher elevations are still waiting for snow to melt, lower-elevations have noticed a shift in the beginning of the growing season. This variability has led the American Robin to begin its altitudinal migration, on average, 14 days earlier than it has in the past. The yellow-bellied marmot, which lives year round at high elevations, is also emerging from hibernation 38 days earlier each year due to increased springtime temperatures on the mountainside (Inouye *et al.*, 2000). Upon emergence, or arrival, these animals face serious ecological problems if plants have received enough sunlight to be able to produce food as a result of lingering winter snowpacks. Overall, it seems that

species living at elevations with increased levels of winter precipitation face starvation if expected resources are not available during critical life stages.

In contrast, in other regions such as the Himalayan Mountains, the phenology of flowering plants has been altered such that 517 species of rhododendrons are flowering a month earlier than normal (Xu *et al.*, 2009). As precipitation declines in this region the implications for alteration of short-lived resource availability and consequently biotic interactions are huge. Many animals rely of periodically available resources that can be exploited through specialized adaptations. Bees and butterflies in the Himalayas, regular pollinators of rhododendrons, must be able to adapt to significantly shifting flowering times or else their fate and the fate of the rhododendrons' pollen and overall species' survival is unlikely (Xu *et al.*, 2009). This example is just one of the millions of interactions between biota on mountains across the globe that face challenges associated with morphing phenologies due to global warming. Altered pollinator, as well as herbivore and carnivore, relationships are about to drastically change as species adapt or do not adapt to the direct and indirect effects of climate change at varying speeds and degrees. With such high levels of endemism and specificity found at high elevations we can only expect to see amplified alterations to a system no longer controlled by predictable patterns of resource availability.

The disruption of phenological synchrony, especially appropriately timed occurrence of critical life stages, between herbivores and their host plants, or between predators and their prey, may be a key pathway for climate change to impact insect ecology (Watt & MacFarlane, 2002). These disruptions are expected to be enhanced for high-elevation species (Bylund, 1999). As insects can expand their ranges and invade new habitats much more quickly than plant populations, due in part to shorter generation times, we should expect to see changes in the severity, frequency, and spatial distribution of pest outbreaks (Logan, 2003). Associations between important herbivorous animals and the pests they control can go awry. In addition, physical controls such as winter temperatures will no longer become effective if, for example, winters aren't cold

enough to kill the mountain pine beetle decimating pine populations in the Western United States. Pest invasions in which normal ecological restraints no longer apply, invite more chaos onto mountains already reeling from other climate change induced casualties.

DISPERSAL OF DISEASES

The spread of diseases across space occurs along both latitudinal and elevational gradients. As climate change alters the physical environment along these gradients, diseases well-adapted to certain physical parameters may flourish if climate change facilitates the expansion of these abiotic environments. The recent chytrid-thermal-optimum hypothesis suggests that climate change has fostered the spread of the *Batrachochytrium* (chytrid) fungus at mid-elevations along the mountains of the Neotropics (Pounds *et al.*, 2006). As the climate envelope along mid-elevations has narrowed in recent decades, due to daytime cooling and nighttime warming as a result of climate change, the expansion of environments maintaining the optimal temperature for the chytrid fungus has allowed the species to decimate Neotropical amphibian populations. In fact 67% of the 110 species of endemic harlequin frogs (*Atelopus* sp.) of the American tropics went extinct in the late 1980's due to the arrival of the chytrid fungus (Pounds *et al.*, 2006). Scientists propose that temperatures at many highland localities have shifted towards the growth optimum of the chytrid fungus, thus encouraging outbreaks as the range of this disease widens. Despite recent hypotheses the ultimate trigger of said outbreak is still debatable, however. There is currently some uncertainty among scientists if disease-related extirpations are linked to climate change or solely wave-like dispersal patterns expected after introductions of the chytrid fungus into Venezuela in the 1970's (Lips *et al.*, 2008). Despite current dispute, the role of climate change in eroding biodiversity through facilitation of the spread of infectious diseases, especially along mountain chains linked climatically, will continue to encourage scientific study in the future.

DISPERSAL AND GENETIC DIVERSITY

Robert MacArthur and E.O. Wilson defined species richness on islands to be governed by two overarching themes: the isolation effect and the area effect. This fundamental theory of biogeography argues that rates of immigration and extinction, and thus total species richness on islands, to be primarily controlled by proximity to mainland populations and the relative size of each island, respectively (MacArthur & Wilson, 1967). While mountains don't exhibit all of the characteristics of oceanic islands, the area effect seems applicable in both environments as the smaller the mountaintop ranges, the greater the likelihood of extinction for species who reside on the tops of mountains and thus find themselves in a situation in which they have no range into which they can move upslope. The isolation effect for mountaintop species is less understood. A landmark paper in 1971 by James H. Brown found that the diversity and distribution of small mammals on mountain islands cannot be explained in terms of equilibrium between colonization and extinction. In fact Brown believed the rate of immigration of boreal mammals on Great Basin mountaintops to be effectively zero as climatic barriers isolate them in their alpine ecosystems. According to this theory, these active-dispersing mammals are trapped in their island refugia, unable to expand their range into environments, such as desert lowlands, they are ill-adapted to survive or migrate within. In addition they are also face threats which include loss of habitat as their ideal climate moves upwards towards non-existent alpine reaches (Brown, 1971).

The theory of non-equilibrium insular biogeography, explained above, seems reasonable, yet new nuances in the Great Basin ecosystem have emerged to contradict the absolution of isolation amongst these Pleistocene relicts. Researchers studying the genetic diversity of marmot populations across seemingly isolated mountaintops within the Great Basin made a shocking discovery. Genetic diversity and geographic distance of marmot populations were found to be positively correlated, such that nearby but distinct marmot populations were found to be more genetically similar than distinct marmot populations found on mountaintops farther away from each other. In addition,

researchers found higher than expected levels of genetic diversity amongst all distinct populations. This contradicts what earlier research suggested would happen if populations completely isolated were not able to combat the negative ecological consequences of genetic drift and became less genetically diverse (Floyd, Vuren, & May, 2005). As a result, the desert lowlands once thought to be impermeable barriers, seem to have been hospitable enough for marmot migration and thus genetic recombination across lowland, talus foothills.

The results of such research seem promising, however, despite the fact that mountaintop mammal populations can disperse today, in the future it is unlikely they will be able to maintain such movement. The area available to boreal populations is expected to shrink as their habitats shift upslope (Orloci, 1994; Gottfried *et al.*, 1999). This range shift will make the already difficult migration even more challenging. As a result, the probability that immigration will rescue declining populations and thus increase population size and genetic diversity will decline in the future (Floyd, Vuren, & May, 2005). Marmot opulations unable to disperse and thus interbreed will become genetically homozygous and be more susceptible to inbreeding depression. Unfortunately, according to the results of one predictive model, a warming of 3ºC in the Great Basin will cause local extinctions of several boreal mammals and the loss of 50% of mountaintop fauna in many locations (McDonald, 2005).

In a similar study within the American Southwest, researchers looked at the genetic variation in four species of mountaintop mammals: the least chipmunk, the Colorado chipmunk, the red squirrel, and the Mexican woodrat. They found reduced genetic variation including loss of heterozygosity, polymorphisms, and allelic diversity within insular distributions given a global warming scenario (Ditto & Frey, 2007). With such a loss in genetic diversity, species will be less capable of coping with changing environmental conditions, leaving them more vulnerable to extinction as a result of global warming. In concordance to non-equilibrium insular biogeography, the loss of island area dooms genetic heterozygosity. Further increased isolation negatively affects

13

genetic polymorphisms and allelic diversity, all of which increase the probability of population extinctions in both the short and long term (Ditto & Frey, 2007).

While active terrestrial dispersers along mountaintops such as marmots and chipmunks have little to look forward to as a result of climate change, the story may change as the type of dispersing mechanism does. In fact populations of the wind-dispersed Mountain birch in Sweden, which exhibit high levels of genetic diversity, appear to have maintained that diversity as their populations move up in elevation as a result of climate change (Truong, Palme, & Felber, 2007). These populations maintain high gene flow as researchers found little genetic variation among populations and overall increased genetic diversity for the species. High levels of genetic diversity are incredibly important as they help species avoid genetic bottlenecks and genetic drift. As this species of birch has indicated, the individuals moving up in elevation are able to maintain their species diversity due to low spatial genetic structure within populations and extensive gene flow across the rising altitudinal range of the species (Truong, Palme, & Felber, 2007). As passive dispersers utilizing wind-energy are able to maintain immigration essential for species richness on mountains, while active dispersers forced to the tops of mountains are not, it appears that plants such as the mountain birch are better equipped to avoid extinction in the face of a changing climate.

CONCLUSION

Understanding the way species are able to move across space as our climate warms can help us understand the biological realities facing mountain species in the coming years. While the biological outcomes will be complex, certain patterns emerge that can help conceptualize the future for many mountain ecosystems. The phenomenon of upslope displacement correlates to precarious futures for mountaintop endemics running out of a range. The indirect effects of warming sea surface temperatures will also act to destroy global biodiversity as global climate change drastically modifies elevationally-driven microclimates that control glacial meltwaters and orograhpic clouds. Similarly, the

phenology of lowland and highland species will be disrupted as the natural forcings of climate change act upon elevational climates in different ways. Additionally, dispersal mechanisms will both amplify the chance for disease outbreaks across widening elevational gradients, and limit the immigration of mountain species unable to maintain genetic diversity through lowland migration routes. In conclusion, striving to predict and interpret the biogeographical mechanisms of climate change that effect mountaintop species will help scientists better understand the fate of the flora and fauna of the mountains of the world today.

LITERATURE CITED

Brown, J.H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. *The American Naturalist* 105(945): 467-478.

Brown, L.E., Hannah, D.M., Milner, A.M. 2007. Vulnerability of alpine stream biodiversity to shrinking glaciers and snowpacks. *Global Change Biology* 13: 958-967.

Bylund, H. 1999. Climate change and outbreaks of geometrid moths in the North. *Vaxtskyddnotiser* 63: 5-9.

Colwell, R.K., Brehm, G., Cardelus, C.L., Gilman, A.C., Longino, J.T. 2008. Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science* 322: 258-261.

Davis, M.B., Botkin, D.B. 1985. Sensitivity of cool-temperate forests and their fossil pollen record to rapid temperate change. *Journal of Quaternary Science* 23(3): 327-340.

Ditto, A.M., Frey, J.K. 2007. Effects of ecogeographic variables on genetic variation in montane mammals: implications for conservation in a global warming scenario. *Journal of Biogeography* 34: 1136-1149.

Floyd, C. Vuren, D, May, B. 2005. Marmots on Great Basin mountaintops: using genetics to test a biogeographic paradigm. *Ecology* 86(8): 2145-2153.

Gottfried, M., Pauli, H, Reiter, K, Grabherr, G. 1999. A fine-scaled predictive model for changes in species distribution patterns of high mountain plants induced by climate warming. *Diversity and Distributions* 5:241-251.

Hill, J.K., Thomas, C.D., Fox, R., Telfer, M.G., Willis, S.G., Asher, H.J., Huntley, B. 2002. Responses of butterflies to twentieth century climate warming: implications for future ranges. *Proceedings of the Royal Society of London Series B* 269: 2163-2171.

Huntley, B. 1990. European vegetation history: Palaeovegetation maps from pollen data - 13000 yr BP to present. *Journal of Quaternary Science* 5:103–122.

Inouye, D.W., Barr, B., Armitage, K.B., Inouye, B.D. 2000. Climate change is affecting altitudinal migrants and hibernating species. *Proceedings of the National Academy of Sciences* 97(4): 1630-1633.

Intergovernmental Panel on Climate Change. 2007. *Climate change 2007 synthesis report: Summary for policy makers*. Intergovernmental Panel on Climate Change, Geneva, Switzerland.

Kullman, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology* 90: 68-77.

Lips, KR., Diffendorfer, J., Mendelson III, J.R., Sears, MW. 2008. Riding the wave: reconciling the roles of disease and climate change in the amphibian declines. *PLoS Biology* 6(3): 441-455.

Logan, J.A., Regiere, J., Powell, J.A. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology* 1(3): 130-137.

MacArthur, R.H., Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, NJ.

McDonald, K.A., Brown, J.H. 1992. Using montane mammals to model extinctions due to global climate change. *Conservation Biology* 6: 409-415.

Orlci, L. 1994. Global warming: the process and its anticipated phytoclimatic effects in temperate and cold zones. *Coenose* 9: 69-74.

Raxworthy, C.J., et al. 2008. Extinction vulnerability of tropical montane endemism from warming and upslope displacement: a preliminary appraisal for the highest massif in Madagascar. *Global Change Biology* 14: 1703-1720.

Sekercioglu, C.H., Schneider, S.H., Fay, J.P., Loarie, S.R. 2008. Climate Change, Elevational Range Shifts, and Bird Extinctions. *Conservation Biology* 22: 140-150.

Song, M., Zhou, C., Ouyang, H. 2005. Simulated distribution of vegetation types in response to climate change on the Tibetan Plateau. *Journal of Vegetation Science* 16: 341-350.

Still, C.J., Foster, P.N., Schneider, S.H. 1999. Simulating the effects of climate change on tropical montane cloud forests. *Nature* 398: 608-610.

Truong, C., Palme, A.E., Felber, F. 2007. Recent invasion of the mountain birch *Betula pubescens* ssp. *tortuosa* above the treeline due to climate change: genetic and ecological study in northern Sweden. *European Society for Evolutionary Biology* 20: 369-380.

Prentice, I.C. 1986. Vegetation response to past climatic variation. *Vegetation* 67:131–141.

Prentice, I.C., Bartlein, P.J., Webb, T. 1991. Vegetation and climate change in eastern North America since the last glacial maximum. *Ecology* 72:2038–2056.

Pounds, J.A., et al. 2006. Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439: 161-167.

Pounds, J.A, Fogden, P.L., Campbell, J.H. 1999. Biological response to climate change on a tropical mountain. *Nature* 398: 611-615.

Watt, A.D., McFarlane, A.M. 2002. Will climate change have a different impact on different trophic levels? Phenological development of winter moth Operophtera brumata and its host plants. *Ecological Entomology* 27: 254–56.

Xu, J., Grumbine, R.E., Shrestha, A., Eriksson, M., Yang, X., Wang, Y., Wilkes, A. 2009. The melting Himalayas: cascading effects of climate change on water, biodiversity, and livelihoods. *Conservation Biology* 23(3): 520-530.