The Vulnerability of Biodiversity to Rapid Climate Change

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Synopsis

Over recent decades, conservation biologists and land stewards have become increasingly aware of the need to incorporate rapid changes in climate as a threat to biodiversity in conservation planning and practice. This chapter (1) generalizes future outlooks for climate and discusses uncertainties in these outlooks, (2) reviews key aspects of the vulnerability of biodiversity to climate change, considered from genetics through landscapes, and (3) concludes presenting strategies for handing this vulnerability and associated uncertainty in conservation planning. In summary, biodiversity is vulnerable to changing climate conditions across its breadth and depth—that is to say, altering composition, structure, and function of species genetics and populations and of communities, ecosystems, and landscapes. This vulnerability is highly interwoven across these levels and across temporal and spatial scales, as well as being context dependent. Consequently, the task of incorporating climate vulnerability into conservation planning is essential but challenging. Inherent limitations in predicting outcomes of vulnerability's complex dynamics, coupled with uncertainties in future forcings, make it difficult at best to anticipate specific consequences. A 'vulnerability approach' to conservation planning focuses on enhancing species and ecosystem adaptive capacity, employing strategies to lower risks from uncertainties. Complementary strategies—some analogous to financial and business planning tenets for coping with uncertainty—include expert elicitation, multiple planning horizons, scenario planning, a no-regrets goal, and adaptive management.

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Glossary

Adaptive capacity – Species and system potential for resistance and resilience to environmental change; where resistance is the ability to resist a change in state and resilience is the ability to recover from a change in state following a perturbation.

Biological diversity (Biodiversity) – Complexity in biotic composition, structural, and function considered at levels of species (and their genetics), communities, ecosystems, landscapes, and broader scales.

Microevolution – Evolutionary change (change in gene frequency over generations) within a species or its populations.

Rapid climate change – In the context of this chapter, all features of local and regional surface climate whose attributes may plausibly vary over decadal through centennial scales at rates disruptive to the ecology of species and their physical and biotic environments.

Vulnerability – System or species sensitivity to an environmental change relative to level of exposure to that threat.

Keywords

biological diversity; climatic change; climate vulnerability; conservation biology; ecosystem change; financial investment analog; microevolution; no-regrets strategies; scenario planning; species adaptive capacity; uncertainty; vulnerability assessment

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1.0 Introduction

Over recent decades, conservation biologists and land stewards have become increasingly aware of the need to incorporate rapid changes in climate as a threat to biological diversity ('biodiversity') in planning and management (Comer et al. 2012; Game et al. 2010; Glick et al. 2011; Hannah et al. 2002a; Hansen et al. 2003; Joyce et al. 2009; Mawdsley et al. 2009; National Park Service 2010). This need has intensified as we better understand the multidimensional vulnerability of the biosphere to this and other threats (Rosenzweig et al. 2007; Walther et al. 2002) and the societal consequences of biodiversity loss to ecosystem services (Chapin et al. 2000; Fischlin et al. 2007). Simultaneously, we better appreciate the large uncertainties in foreseeing future states of species and their landscapes and corresponding difficulties in incorporating vulnerability to changing climatic conditions in natural resource management plans (Kittel et al. 2011c; Lawler et al. 2010).

In this chapter, I start by presenting generalized outlooks for and uncertainties in climatic and biotic futures to provide context for discussions in subsequent sections (Section 2.0). The core of the chapter is a review of key aspects of the vulnerability of biodiversity to climate change, considered from species—and their genetics—through community and ecosystem dynamics (Section 3.0). My thesis is that this vulnerability is highly complex—running through all levels of biodiversity—and arises from ecological and evolutionary processes that are strongly interactive, span a wide range of temporal and spatial scales, and are context dependent. Inherent limitations in predicting outcomes of such complex dynamics, coupled with uncertainties in future forcings, make it difficult at best to anticipate specific consequences of this vulnerability. I conclude the chapter presenting strategies for handing such uncertainty in conservation planning (Section 4.0).

2.0 Outlooks for Future Environments

2.1 Future Climate: Outlooks and Uncertainty

The vulnerability of species or ecosystems can be considered in terms of resistance (to changing state) and resilience (ability to recover) to changing climatic conditions and so are relative to the magnitude of the threat. In this regard, I refer to 'rapid climate change' as meaning all features of local and regional surface climate whose attributes may plausibly vary over decadal through centennial scales at rates disruptive to the ecology of species and their physical and biotic environments. An assessment of the vulnerability of current biodiversity to such variation will only be useful to the extent we can specify what the spectrum of plausible future climates might be. For this, we can look to three approaches: historical shifts, model sensitivity, and novel possibilities. The bottom line is that these approaches provide key insights and yet have high uncertainty associated with their spatial and temporal outlooks.

2.1.1 Historical understanding

Forward-looking biotic assessments can draw from analyses of historic periods with rapid climate shifts, such as multidecadal climatic (and linked ecological) regime changes (e.g., the Pacific Decadal Oscillation:Mantua et al. 1997; Pederson et al. 2006). Such an analog approach asks what would be the status of biodiversity if regional climates were to undergo shifts today similar to those observed over past periods, and looks from this point forward, placing these changes in the context of additional threats such as invasive species, exploitation, and habitat degradation.

The primary advantage of the historical approach is that it provides an observation-based assessment of biotic sensitivity to a known forcing. A key limitation is that the past is an imperfect analog of the future—that is, future changes will likely differ in magnitude and character from those in historical or paleo records.

2.1.2 Guarded lessons from modeling

We can glean overarching lessons from climate model sensitivity studies, such as under scenarios of increasing greenhouse gases, sulfate aerosols, and land cover change (e.g., Avila et al. 2012; Feddema et al. 2005; Meehl et al. 2007). Caution is needed, however, in extracting these lessons because of high uncertainty associated with model projections. By 'high,' I mean where the uncertainty is as great as or greater than system sensitivity. This uncertainty is derived from:

- Climate system complexity limiting our ability to model climate (Knutti 2008; Rial et al. 2004).
- Uncertainty in future human forcings on climate such as those determined for various future demographic, economic, and political scenarios (as illustrated by the breadth of possible societal futures in Forster et al. (2007)).
- Limited inclusion of the full complement of human forcings in most climate model experiments (which usually emphasize greenhouse-gas and aerosol forcing) (National Research Council 2005; Pielke 2005; Pielke 2008).

Climate model experiments, nonetheless, convey a fundamental lesson: climate system sensitivity to a host of current and potential future anthropogenic forcings is of a magnitude and rate to raise the prospect for substantial ecological impacts with consequences for the conservation of biodiversity. While we cannot with any certainty anticipate geographic details regarding the sign or size of these effects, the very character of regional climates may likely be altered over the next decades in some generalizable but crucial ways. These entail:

- Multivariate change—including in, but not restricted to, surface temperature and precipitation. Cloud cover (and light regime), wind regime, and other parameters would be expected to change concurrent with temperature and precipitation; however, regional correlations among these variables might not hold as climate patterns shift. Minimum and maximum temperatures would also likely show different responses, as they are partly controlled by different night and daytime processes.
- Changes over a spectrum of ecological timescales—that is, changes not only in annual means, but also in extremes, seasonality, and interannual variability, such as associated with El Niño–Southern Oscillation (ENSO, Meehl et al. 2007).
- Changes shifting over time—for example, trends are not likely to be monotonic if circulation patterns shift in and out of a region or if the climate system passes thresholds or potentially irreversible 'tipping points' (Overpeck and Webb 2000; Schellnhuber 2009).

These plausible changes are of a magnitude and nature to jeopardize the persistence of species, structure of biological communities and food webs, and functioning of ecosystems (Fischlin et al. 2007; Kundzewicz et al. 2007).

2.1.3 Novel climates

Changes in so many aspects of climate suggest the possible formation of novel climates, that is, climates with combinations of conditions with no current analog (Williams and Jackson 2007). The prospect that current environmental niches would disappear and new, reconfigured ones arise places a caveat on our reliance on previously observed relationships of climatic controls over species and ecosystem dynamics. This outlook challenges us to contemplate future states beyond those experienced or expected, including less probable but still plausible futures (Peterson et al. 2003; Turner et al. 2003).

2.2 Climatic Vulnerability of the Physical Environment

In addition to direct effects of climate on organisms, changes in climatic conditions could modify physical components of aquatic and terrestrial environments, with indirect consequences for species and ecosystems (Figure 1, upper left panel). Changing regional and local climates could alter landforms, drainage patterns, soil development, physical and chemical attributes of aquatic systems, and physical disturbance regimes—rearranging or opening up new habitats. Key geophysical processes include:

- Modified surface-water and groundwater hydrology. In winter-snow environments, for example, reduced snowpack and earlier spring snowmelt from warming can result in seasonal shifts in riverine hydrographs (Stewart et al. 2005), affecting biologically-important river, wetland, and lake conditions (e.g., water level, temperature, nutrient and sediment load, and dissolved oxygen) (Poiani and Johnson 1991; Strayer and Dudgeon 2010).
- Shifting atmospheric circulation patterns—altering ocean and lake circulation, sea ice flows, and aeolian transport (of nutrients, propagules, etc). Ocean and lake circulation changes can in turn modify the horizontal distribution of plankton (including larvae) and, coupled with altered surface heat fluxes (e.g., from warmer air temperatures), affect thermal stratification and vertical mixing of nutrients. Such horizontal and vertical structural shifts can alter marine and lacustrine food webs (Brander 2007; Harley et al. 2006).
- Altered geomorphology—from climate-forced catastrophic and cumulative processes. The former include slope instability and flooding arising, for example, from increases in storm frequency and intensity or from rapid deglaciation due to warming—with effects on upland and channel or shore geomorphology (Evans and Clague 1994; National Research Council 2010). Cumulative processes include water and aeolian erosion and deposition, whose changes result in shifting landscape patterns of aggrading and degrading soils and sediments—altering drainage networks, soil structure (creating Entisols and buried horizons, for example), and water quality (e.g., from high sediment loads) (National Research Council 2010; Soil and Water Conservation Society 2003).
- A shift in ice-dominated environments to a net thaw regime. Periglacial landscapes are an example of geomorphological surfaces that are highly sensitive to climate. As complexes of thermokarst terrain with permafrost soils and thaw lakes, these landforms exhibit both stabilizing and destabilizing interactions under increasing temperatures. Their fate depends on positive and negative feedbacks among (1) temperature change, (2) changing snowpack and vegetation (and their interaction), affecting their insulation of the soil surface, (3) soil erodibility, and (4) drainage (Kittel et al. 2011b; van Cleve et al. 1991). With respect to drainage, for example, slope inclination largely determines whether permafrost degradation

under warming results in an expansion of wetlands and thaw lakes (from ground subsidence on low slopes) or in wetland loss and drying soils (from drainage on steeper slopes no longer impeded by impermeable permafrost) (Rouse et al. 1997). In glacial environments, increased melting of glacial ice with warming alters downstream chemistry, such as through enhanced weathering rates due to increased meltwater contact with subglacial rock and, with receding glacial cover, altered microbial (biogeochemical) processes in newly exposed sediments (Baron et al. 2009).

- Other climate-dependent physical disturbance mechanisms—such as changes in frequency and intensity of forest windthrow and 'fire-climate' conditions leading to wildland fires, affecting ecological disturbance regimes (O'Donnell et al. 2011; Schlyter et al. 2006).

Such physical perturbations may force wholesale changes to biotic communities and their landscape patterns (Figure 1, upper panels), facilitating rapid shifts in communities that might otherwise persist under changing local and regional climates.

2.3 Future Outlooks: Biotic Consequences

We can take key lessons about biodiversity's vulnerability to plausible future climate changes from field, laboratory, remote sensing, and modeling studies (Botkin et al. 2007; Chapin et al. 2000; Rosenzweig et al. 2007; Walther 2010). As with climate outlooks, we cannot foresee the details—timing, distribution, or nature—of future ecological outcomes with any certainty. This uncertainty similarly arises from (1) ecological system complexity limiting predictability, (2) uncertainty in future climatic forcing and feedbacks, and (3) limited accounting for synergisms with other environmental stressors in climate impact assessments.

Nonetheless, in the context of generalizations about near-future regional climates presented earlier (Sections 2.1.2 and 2.1.3), we can derive similar generalizations from observations and models about how biodiversity might be altered over the next decades. In broad but significant ways, these include:

- Shifting geographic ranges of marine, continental-water, and terrestrial species (Harley et al. 2006).
- Altered species phenologies (Root et al. 2005; Wolkovich et al. 2012).
- Species interactions spatially and temporally out of phase—altering food webs, competitive interactions, and mutual associations (e.g., pollination) (Both et al. 2009; Jha et al. 2012).
- Changing community structure—potentially giving rise to novel ecosystem types (Overpeck et al. 1992; Seastedt et al. 2008; Urban et al. 2012).
- Changes in ecosystem function—altering biophysical and biogeochemical processes, including primary production (Nemani 2003).
- Disruption of ecosystem services—affecting societal use of resources as water, food, etc. (Cardinale et al. 2012; Chan et al. 2011; Fischlin et al. 2007).

Temporal behavior of these ecological responses will generally follow not only from climatic (and other) forcing, but also from internal stabilizing or non-equilibrium dynamics. The result being:

- A new equilibrium, inasmuch as such has existed historically, would be long in coming, pending first climatic and then ecological stabilization (e.g., at centennial scales)—resulting in extended periods dominated by seral stages.
- Following from shifting climate regimes, ecological changes would not be monotonic—with no single specific outcome developing and persisting over the long term (e.g., no 'winner' or 'loser' species).
- Internal dynamics would exhibit system lags, regime shifts, and tipping points (Allen and Holling 2010; Biggs et al. 2009; Jones et al. 2009; Metzger et al. 2009).

These potential outcomes arise from the fundamental nature of biodiversity and its climatic vulnerability. Processes and factors controlling this vulnerability are explored next.

3.0 Nature of Biotic Vulnerability

3.1 Vulnerability Across the Biodiversity Hierarchy

Biodiversity broadly includes complexity across levels of biotic organization from genetics and populations to communities, landscapes, and ecoregions (and so on). Within these levels, biodiversity also includes complexity with respect to composition (elements present), structure (arrangement of elements), and function (interactions among elements) (Noss 1990). The structure and function of genetic through ecoregional diversity contribute to the maintenance of species diversity and are themselves established as important conservation goals (Groves et al. 2002). Biodiversity is vulnerable to climate across this hierarchy in complex and highly interactive ways (Fischlin et al. 2007; Walther et al. 2002). This section starts with a species-level approach to climate vulnerability, focusing on a species' adaptive capacity and its links to genetic diversity, and then discusses community and ecosystem vulnerability, landscape connectivity, and synergisms with other threats.

3.2 Species Adaptive Capacity

3.2.1 Species Ecology

Physiological Range

A species' adaptive capacity—that is, the potential for resistance and resilience to environmental change—arises from flexibility in its ecological relationships (Figure 1, middle left panel). On first consideration, such flexibility with respect to climate is tied to the breadth and shape of physiological response curves—such as with respect to interacting thermal, moisture, light, chemical (nutrients, salinity), and other climate-linked environmental conditions. Broad physiological optima will support species resistance; while species with narrow physiological limits are subject to catastrophic responses (e.g., tropical organisms with little freeze tolerance). (The genetics of broad versus narrow climatic optima is discussed later on.) In addition, physiological tolerances change with life stage in many species (Harley et al. 2006), so that vulnerability may be linked to a critical time or may shift among factors during an organism's lifespan.

Species Interactions

The link between a species' adaptive capacity and physiology may, however, be muddled by interactions with associated species, including competitors, predators, prey, mutualists, and

pathogens (Figure 1). Consequently, species vulnerability may be just as much determined indirectly via climate responses of associates (and so by altered community compositional and structural diversity) as by direct forcing of a changing climate. The impact of community restructuring (discussed later) on a species' vulnerability propagates in through trophic and other ecological networks—that is, from beyond the species' most immediate connections. Altered interspecific interactions can ameliorate a species' vulnerability, such as through competitive release, or exacerbate it as from reduced resource availability. Species with high adaptive capacity:

- Can readily shift resource utilization under shifting competitive and trophic environments.
- Are not highly dependent on mutualistic relationships (or at least not with species lacking matched adaptive capacity) (Hughes et al. 2003; Jha et al. 2012).
- Have resistance (expressed or latent) to emergent diseases.

Population Viability

Population dynamics also determine species vulnerability Figure 1). Direct climatic impacts on reproduction and mortality rates alter population viability across a range of timescales (e.g., from hourly events to decadal variability). Such controls over population size are manifested as both density-independent climate effects (as from catastrophic events) and density-dependent effects (where the climate impact depends on, for example, the magnitude of intraspecific competition for food, shelter, and mates). At weekly scales, for example, changes in frequency and timing of severe winter storms can have both density-independent and dependent effects on large mammal survivorship (Berger 1983; Hallett et al. 2004).

Both animals and plants exhibit climate-induced shifts in reproductive traits affecting population dynamics, such as fecundity, generation time, breeding/flowering season, and other phenological traits (Inouye 2008; Isaac 2009; Post et al. 2001). How traits respond to climate and the consequences for population viability depend on a species' overall life-history strategy—such as for r- versus K-selected species, generalists versus specialists, and for different mating systems; in these contrasts, similar climatic behavior can generate opposite outcomes (Isaac 2009).

Population viability is also tied to species interactions, as those discussed above. At seasonal scales, reproduction and survivorship are altered by loss of phenological synchrony between:

- A species' climate-cued life-history events and climate-cued trophic resource availability, as seen in migratory and winter-dormant vertebrates (Both et al. 2009; Forchhammer and Post 2004; Harrington et al. 1999; Inouye et al. 2000).
- The climate-cued life-history events of mutualists, as for plants and their pollinators (Jha et al. 2012).

At interannual and longer scales, climate affects predator–prey population cycles—such as that involving Canadian lynx and snowshoe hare (Stenseth 2007)—and climate-regulated host–disease dynamics, as in insect herbivore–parasitoid systems (Hance et al. 2007; Stireman et al. 2005) and plant host–pathogen interactions (Brasier and Scott 1994; Woods et al. 2005).

The constraints imposed on adaptive capacity by intra- and interspecific interactions tend to narrow a species' range relative to its potential climatic limits based on physiology alone. If changing

population and community dynamics shift these constraints, a species may reveal latent capacity to fill niches that are consistent with its physiological limits but from where it has been excluded.

3.2.2 Dispersal Capacity and Range Shifts

Vulnerability also depends on a species' ability to disperse away from sites becoming less favorable to improving ones—that is, to successfully track suitable conditions as they shift across a landscape or region (Figure 1, middle left panel). While the potential for species range shifts is often evaluated with empirical 'climate envelop' or environmental niche models, dispersal success is tied to dispersal life history strategies and interspecific interactions generally not incorporated in these models (Davis et al. 1998; Wiens et al. 2009) (however, see Anderson et al. 2002; Keith et al. 2008).

Even within taxonomic groups, species differ in dispersal attributes, which set their potential for keeping up with elevational or lateral shifts in climates (Chen et al. 2011; Urban et al. 2012). Species factors include:

- Capacity for diffusive or jump dispersal, whether by self-locomotion or facilitation by wind, water, or other species.
- Establishment life-history strategies (e.g., reproductive rates, competitive abilities, and adult survivorship associated with early versus late successional species).

Successful dispersal is also a function of environmental conditions along the way. Source–to–sink abiotic and biotic site factors include:

- A species' current distribution and population size (source strength), including persistent relict populations existing outside of its generalized climatic range (Botkin et al. 2007).
- Landscapes en route presenting physiographic or biotic barriers and corridors (including limitations or opportunities offered by human-modified domains).
- Suitability of potential sink habitats in terms of their abiotic, trophic (food resources, predator), and competitive setting (Urban et al. 2012).

Species whose in situ adaptive capacity is low—and thus vulnerable to local extirpation—and additionally are poor dispersers and isolated from emerging favorable sites by physiography or human landuse are additionally vulnerable to extinction (Figure 1, bottom left panel). While these processes look at the leading edge of range shifts, demographic factors and reproductive traits (e.g., longevity, cloning) and disturbance tolerance are species-specific controls over lags (species persistence) at the trailing edge (Elliott-Fisk 1983; Hampe and Petit 2005).

Species differences in adaptive capacity in general and dispersal ability in particular would lead to differential rates of range movement under a shifting climate (and disturbance) regime. A resulting mixture of colonizing, lagging, and declining species will contribute to community structural disruption, the predominance of seral (successional) associations, and, potentially, to the rise of novel communities (Figure 1) (Urban et al. 2012; Williams and Jackson 2007). The nature and rate of community change will depend on:

- Relative 'openness' of the current community—versus one presenting a highly competitive environment.
- Climate vulnerability—and hence degree of persistence—of dominant and keystone species that maintain existing community structure.

- State-changing disturbance (fire, insect outbreaks).
- Dispersal and establishment abilities of arriving species.

Under slow rates of climatic change, communities may maintain their composition but alter their relative structure, at least in the shorter term (Breshears et al. 2008; Kelly and Goulden 2008). However, under high disturbance with rapid changes in local climate, communities may collapse, presenting open environments to arriving species. Community structural vulnerability is discussed further in Section 3.3.1.

3.2.3 Phenotypic Plasticity

Phenotypic plasticity can shift adaptive capacity under a rapidly changing climate without relying on genetic variation (Reed et al. 2011; Rice and Emery 2003). Requirements for adaptive phenotypic plasticity are that:

- environmental cues are sufficiently reliable to trigger plastic responses,
- plastic responses sufficiently track the pace and breadth of environmental changes,
- fitness benefits exceed costs of maintaining plastic potential (Reed et al. 2011).

The degree of plasticity varies widely among taxa. For some species, adaptive plasticity is not sufficient to optimize fitness throughout a species' current climatic range (e.g., as seen for a temperate-grassland annual forb in a reciprocal transplant study, Etterson 2004a), potentially leading to reduced local population viability under a shifting climate. For others, it may be as great as to accommodate wide climatic shifts. For example, over the Pleistocene glacial–interglacial cycle, a kangaroo rat species largely maintained its current distribution by shifting its realized niche likely through phenotypic plasticity, rather than with genetic change (Jezkova et al. 2011).

3.2.4 Geographic Gradients in Adaptive Capacity

Genetic Differentiation Across a Species' Range

As the underlying basis for adaptive capacity, genetic make-up sets the vulnerability of a species to a changing environment. However, abiotic and biotic constraints on populations tend to affect a species' adaptive capacity differently at range extremes and at extremes versus in its core, applying different selective pressures and driving geographic genetic differentiation (Bentz et al. 2001; Case and Taper 2000; Davis et al. 2005; Etterson 2004b; Hampe and Petit 2005; Howe et al. 2003). Consequently, physiology, life history, and other (genetic-based) elements of adaptive capacity may differ substantially for populations at the core of a species' distribution versus those at its limits. Such populations may then have different responses to similar climatic change. A species' vulnerability then varies geographically not only with varying availability of suitable habitats, but also with location-specific genetically determined capacity to adjust to new local niches (e.g., Etterson 2004b; Rehfeldt et al. 1999).

A consequence of this geography is that populations in the core of a species' range may be maladapted to its marginal climates. Such a 'core population' may not be viable under a climate shift that brings it near to, but still within, the limits of the species' current climate range. Under these conditions, empirical niche (climate envelop) models would overestimate a species' persistence.

Role of the Past

Biogeographic history (how species got to where they are now) and evolutionary history (how they changed along the way and once there) are determinants of current genetic geography. Regional climatic history plays a role in such geographic differentiation. For example, it can act to reduce local genetic diversity under diametric conditions of:

- steady climate regimes, through stabilizing selection (Rice and Emery 2003),
- rapid climate change or severe events (such as sustained drought), creating genetic bottlenecks.

In both of these cases, past conditions potentially reduce current adaptive capacity and increase local vulnerability to future climate shifts. Effects of climatic variability on genetics are discussed further in the next section.

3.2.5 Shifting Adaptive Capacity in Time: Microevolution

Direct abiotic and indirect biotic forcing associated with a changing climate apply corresponding selective pressures; the question is whether these pressures can sufficiently shift population genetics at ecological timescales to reduce species vulnerability. Microevolution, that is, evolutionary change within a species or its populations, has allowed some taxa to adapt to recent human-forced environmental change, including altered climatic conditions (reviewed in Rice and Emery 2003). This is to say, that genetic shifts in populations that maintain their viability can occur at rates matching rapid environmental change. Consequently, evolutionary rates may be large enough for some species to adapt to rapidly changing local climate, reducing the probability of their extinction (Reed et al. 2011; Rice and Emery 2003).

Climatic Selective Pressures

Climate-linked selective pressure produces three generalized outcomes as a function of climatic temporal behavior (Reed et al. 2011; Rice and Emery 2003):

- Climatic consistency gives rise to stabilizing selection reducing generic diversity, in turn reducing adaptive capacity, as mentioned earlier.
- Directional change in climatic conditions supports net directional selection, shifting adaptive capacity. However, rapid climate shifts exert strong selective pressure which may exceed microevolutionary potential (discussed shortly). A consequence of strong selection is high levels of mortality. This may make even currently robust populations vulnerable by diminishing their size and condition to levels where they become subject to stochastic fluctuations in numbers and genetics (genetic drift) (Reed et al. 2011). This threat to population viability may occur even as directional selection is moving phenotypes to a new environmental optimum in the remaining population.
- If climatic variability increases in a way that gives inconsistent direction to selection pressures, it can disrupt both stabilizing and directional selection. This would lead to poor climatic optimization and reduced adaptive capacity. Alternatively, increased variability can promote selection for phenotypic plasticity, but only if the altered climate regime has a predictable element that be relied on as an environmental cue—a required condition for plasticity noted earlier. Without this predictability, however, plasticity would be less reliable and so less favored under increased climate variability (Reed et al. 2011).

Strong environmental perturbation can, in addition, trigger release of cryptic genetic variation—variation present but otherwise not phenotypically expressed (Gibson and Dworkin 2004; McGuigan and Sgrò 2009). Such a release produces novel, potentially adaptive phenotypes (Hayden et al. 2011). Suggested trigger mechanisms are through environmental disruption or genetic mutation (which itself can be induced by environmental stress, Reed et al. 2011).

Factors Controlling Microevolution

Microevolution is limited by (1) genetics, (2) reproductive biology and demographics, and (3) coevolutionary processes (Rice and Emery 2003). Genetic factors which constrain or facilitate microevolution include:

- Local genetic diversity, providing either a genetic source for adaptive shifts or a drag from genetic load (suboptimal genes reducing fitness).
- Metapopulation gene flow, which can provide a population with either (1) genotypes well adapted to new conditions or (2) maladapted genes more suited to the source location and so adding genetic load (i.e., antagonistic gene flow).
- Phenotypic plasticity, discussed earlier, which can buffer the negative effects of strong selective pressure and allow time for genotypes to track environmental shifts.
- Positive or negative genetic correlation among adaptive traits (which each support an optimal phenotypic response to an environmental change) can accelerate or hinder selection relative to traits that act independently. Traits which act in concert (through synergistic genetic interaction) promote adaptive change. On the other hand, with negatively-correlated traits, promotion of one trait reduces selection for the other. Such antagonistic genetic interaction makes directional selection ineffective in optimizing a phenotype to a consistently changing environment (Etterson and Shaw 2001). Genetic interactions are further complicated when traits that are positively correlated under selection favoring some phenotypes are negatively correlated in selection favoring others (Snitkin and Segrè 2011).

On this last topic, positive genetic correlations may not be stable under multivariate environmental change, where selective pressure is for phenotypes to track multiple shifting optima (Reed et al. 2011). Additionally, under the development of shifting or novel climates, a breakdown of currently reliable correlations among environmental variables (such as between temperature and day-length seasonality) may disrupt current positive genetic correlations (such as among traits setting cold-season acclimation in temperate and boreal plants, Howe et al. 2003).

Microevolutionary factors related to reproductive biology and demography include:

- Environmentally-cued shifts in sexual versus asexual reproduction in plant, animal, and microbial taxa (Chen and McDonald 1996; Elliott-Fisk 1983; Hughes et al. 2003).
- Generation time, fecundity, and population size—where short generations, many offspring per generation, and large populations contribute to higher population growth potential, facilitating adaptive evolutionary shifts (Hughes et al. 2003; Reed et al. 2011).

- Reproductive longevity of adults and viability of dormant propagule reservoirs (e.g., seed banks)—which can provide either genotypes that have come around again to be well adapted or ones that increase genetic load (Hughes et al. 2003; Rice and Emery 2003).

Coevolutionary selective pressures arise from shifting trophic, mutualistic, or epidemiologic interactions. These pressures may be particularly crucial when one species' microevolutionary response is tightly constrained by the adaptive capacity of and concurrent (but not necessarily matching) evolutionary changes in coevolved associates (Holt 1990; Rice and Emery 2003).

3.3 Vulnerability of Community Structure and Ecosystem Function

3.3.1 Structure

Response of communities to a changing environment is determined not only by species' individual responses to external forcing, but also by internal dynamics. Community structural changes (composition, richness, evenness) arise from the relative strengths of such forcing and species interactions. Three paths are determined by the dominance of: (1) physically disruptive climate forcing, (2) weak biotic interactions, or (3) strong, system-defining biotic interactions (Figure 1, upper left panel).

In the first case, climate drives catastrophic or cumulative changes to the physical environment sufficient to disrupt the integrity of a community (as previously discussed). Primary or secondary succession will give rise to potentially novel sequences of communities under new, shifting abiotic (climate, disturbance regime) and biotic (e.g., arriving species) conditions.

Under a climate that is not so disruptive to the physical habitat, community responses to climate depend on the strength of interactions among species (Chapin et al. 2000). In communities where species belong to fairly generic functional groups and interactions are weak (that is, flexible among roughly substitutable species), community structure is affected by an overall shifting presence and abundance of species as they respond to climate and to trophic, mutualistic, and competitive interactions. In this case, communities adjust primarily 'bottom up'—progressing up trophic networks in response to, for example, changes in primary producer or microbial decomposer populations, the principal facilitators of system energy or nutrient flows (Chapin et al. 2000; Harrington et al. 1999; Inouye 2008; Mantua et al. 1997; McGowan 1998; Walther 2010).

In communities with strong interactions, on the other hand, structural changes may be determined by the presence and abundance of single species—such as for keystone taxa, whose presence or loss cascades 'top down' through trophic levels (Chapin et al. 2000; Power et al. 1996; Walther 2010). In general, such species-sensitive restructuring occurs where:

- Mutualistic, trophic, or competitive interactions are tight—e.g., for animal pollinator–plant interactions, top predators, and grazer-determined plant succession (Collins and Calabrese 2012; Jha et al. 2012).
- A species' traits strongly control system dynamics—such as for species that tightly regulate system resources, disturbance regime, or microclimate (e.g., nitrogen-fixer, low water-use-efficiency, fire-prone, and permafrost-stabilizing plant species) (Chapin et al. 2000; D'Antonio and Vitousek 1992; van Cleve et al. 1991; van Wilgen et al. 1996; Wilson and Agnew 1992).

Within a food web, strong bottom-up and top-down effects may both play a role—with top-down restructuring influencing lower trophic levels and bottom-up simultaneously affecting top levels (e.g., Shurin et al. 2012), potentially in a way that can synergistically contribute to ecosystem stability (de Ruiter et al. 1995).

Emergent versus Species Responses

A straightforward community-level phenological response to shifts in seasonal climate may say little about individual species responses and the consequences for tight species interactions. For example, a lengthening of the growing season for mid- and high latitude terrestrial plant communities could be expected to increase food resources for herbivores. However, this community response is likely emergent from a variety of individual plant species responses—some advancing their phenologies, some with cycles sped up or lengthened, and others with little change (Steltzer and Post 2009). For herbivores, a consequence can be disrupted timing of plant species that provide crucial dietary needs during specific periods of the summer (e.g., in preparation for hibernation) (Hill and Florant 1999; Steltzer and Post 2009).

3.3.2 Ecosystem Function

Climate and Plant Functional Types

Terrestrial biogeochemical processes are largely controlled by moisture and thermal regimes in interaction with soil properties (e.g., water and nutrient holding capacity), vegetation, and geomorphology (e.g., hillslope position) (Band et al. 1993; Daly et al. 2000; Parton et al. 1995). The role of plant community structure and species composition can be generalized by plant functional types that categorize species' contributions to ecosystem physiology and architecture (Smith et al. 1997). Such functional distinctions affect biogeochemical rates through quantity and quality (nutrient versus structural content) of plant matter inputs inherent in contrasts of, for example, annual versus perennial herbaceous, deciduous versus evergreen woody, C_4 versus C_3 photosynthetic pathway, and nitrogen fixing versus non-fixing species. Climate-driven shifts in the diversity of an ecosystem's plant functional types, especially with the gain or loss of key types controlling system dynamics, can be major determinants of the climate response of energy and matter flow rates and pathways (Díaz and Cabido 2001; Kappelle et al. 1999). This sensitivity to shifts in key types can occur even if each type is represented by only one to a few species, resulting in little change in overall species diversity.

Aboveground–Belowground Ecosystem Interactions

Material and energy flows in terrestrial ecosystems are also determined by climate-sensitive interactions between above- and belowground realms and so by traits of these communities (Bardgett et al. 2005; Wall 2007; Wardle et al. 2004). Belowground microbial and faunal communities interact with the aboveground realm in ways that depend on the nature of their association with plants—those in food webs associated with roots (with primary consumption by root herbivores, parasites, and pathogens), in detrital food webs (decomposers), versus in mutualistic association with roots (mycorrhizae) (Bever et al. 2010; De Deyn and Van der Putten 2005; Wardle et al. 2004).

The aboveground community exerts strong control over detrital and root food webs primarily through the quantity and quality of plant matter inputs—a function of plant community

composition, as described above. In addition, aboveground herbivory can alter plant tissue quality—in the short term, through plant biochemical responses (of increased nitrogen content and/or secondary defensive compounds) and, in the long term, through plant community shifts (to lower-quality forage species) (Wardle et al. 2004).

At the same time, belowground communities strongly influence plant productivity (and tissue quality) through:

- The detrital food web, both mineralizing organic inputs to available forms and competing with plants for these nutrients.
- Mycorrhizal facilitation of plant nutrient uptake.
- Degradation of root uptake efficiency by the root-associated food web (through root consumption and disease).
- Belowground microbial and invertebrate induction of plant defenses against aboveground herbivory and plant-shoot pathogens, altering plant growth and chemistry (defensive compounds). Such plant productivity and tissue chemical responses can be both plant- and belowground inducer-species specific and have bottom-up community effects, shifting plant competitive and trophic interactions. (Bezemer and van Dam 2005)

Climatic vulnerability of ecosystems emerges from the compositional and functional diversity of these communities and complexity of their interactions (Chapin et al. 2000; Kappelle et al. 1999; Wardle et al. 2004). Biogeochemical processes and functional group behavior are strongly sensitive to their climatic controls; however, ecosystem model intercomparison studies suggest high uncertainty in our understanding of this vulnerability even at the broadest (regional and continental) scales (Cramer et al. 2001; Purves and Pacala 2008; Schimel et al. 2000). At finer scales, the magnitude and expression of climate vulnerability are even less predictable because above- and belowground dynamics are highly nonlinear and depend on site details, such as soil fertility and, as just described, soil and plant community composition and aboveground herbivory (Wardle et al. 2004). Such nonlinear ecological networks are potentially capable of sudden regime shifts and passing through tipping points in their structure and function (Biggs et al. 2009; Hastings and Wysham 2010; Wall 2007).

3.4 Landscape–Global Continuum

The spatial arrangement of communities and ecosystem processes on the landscape brings additional complexity arising from physical and biotic connectivity. Connectivity of landscape units provides for water- and air-mediated flow of energy and materials (e.g., organic and inorganic particles, water, and propagules) downslope and downwind (Reiners and Driese 2001; Seastedt et al. 2004; Soranno et al. 1999). In addition, landscape continuity facilitates seasonal and ontogenetic (life-stage) migrations and range expansion (Berger 2004; Olds et al. 2012). Such biogeochemical, population, and other linkages are vulnerable to disruption of the physical environment (e.g., shifted hydrology and destabilized landforms, as discussed earlier) and interruption of biotic continuity through rearrangement or loss of crucial communities (such as suitable habitats forming corridors or those that are key sources for transported organic material).

Connectivity extends to regional and global scales with interbasin, intercontinental, and between ocean and continent aeolian transport of aerosols (e.g., nitrogen deposition), dust (from aridlands),

and organisms (e.g., microbes, insects, propagules) (Baron et al. 2009; Brander 2007; Sharma et al. 2007; Washington et al. 2009; White et al. 2012). Sustained changes in such inputs can alter ecosystem function and structure (Avila and Peñuelas 1999; Fenn et al. 2003; Steltzer et al. 2009).

3.5 Synergisms Among Climate and Other Stressors

Climatic impacts on species adaptive capacity are, in addition, in the context of other environmental stressors on biodiversity (Figure 1, upper left panel). These include direct anthropogenic effects such as habitat conversion (e.g., Vieira et al. 2009), exotic invasive introductions ('biotic homogenization,' Olden et al. 2004), and disruption of biogeochemical cycles (Vitousek et al. 1997). Acting together, these stressors exhibit not only additive effects but also strong synergisms with climate (Brook et al. 2008). Exacerbating feedbacks between climate and other stressors include those with:

- Habitat modification—including (1) atmosphere–land surface feedbacks accompanying land use change, such as fragmentation, salinization, and desertification (e.g., accelerated drought with deforestation; Laurance and Williamson 2001) and (2), for aquatic environments, compounding influences of precipitation regime change, upland land use, and water impoundment on light, temperature, sediment load, and chemistry of continental and coastal waters (Walling 2009).
- Overexploitation of species utilized for food, timber, etc.—where reduction or extirpation of populations and disruption of food web dynamics increase a species' vulnerability to other stressors (such as climate) (Biggs et al. 2009; Brander 2007; Nellemann et al. 2008).
- Altered fire disturbance regime—from environmental changes including (1) human-related fire suppression or ignition, (2) shifts to more fire-prone plant communities with the establishment of invasive exotics, and (3) fertilization from atmospheric nitrogen deposition adding fuel load (D'Antonio and Vitousek 1992; Fenn et al. 2003; Schoennagel et al. 2004).
- Altered chemical environment—inducing biogeochemical and community changes from (1) elevated atmospheric CO_2-induced fertilization (of terrestrial plants) and ocean acidification (to the detriment of calcifying marine organisms), (2) introduced toxins via air, soil, and water pollution, (3) atmospheric deposition causing soil and water acidification and enhancing nitrogen inputs (as just noted re fire), and (4) altered terrestrial nutrient runoff to continental waters and oceans (Baron et al. 2009; Brander 2007; Fenn et al. 2003; Gitay et al. 2001; Kleypas et al. 1999; Pandolfi et al. 2011). In terrestrial and aquatic systems, changes in physical climate influence these chemical deposition, infiltration, and runoff impacts (1) directly through shifting precipitation and snowmelt regimes and (2) synergistically, with thermal and moisture regimes also affecting these biogeochemical responses.
- Insect outbreaks—aided by climate directly through: (1) altered host plant susceptibility (e.g., plant moisture status) and (2) altered insect life cycles (e.g., a step-up in the number of breeding cycles per annum) (Mitton and Ferrenberg 2012; Raffa et al. 2008).
- Invasive exotics—with climate-facilitated spread of invasives through, for example, new establishment opportunities arising from shifts in: (1) dispersal routes (via wind and water circulation), (2) disturbance regimes, or (3) competitive setting (from community shifts) (Burgiel and Muir 2010; Hellmann et al. 2008). In a climatic feedback, the impact of invasives on community structure can be strong enough to alter basin microclimates and hydrology (van Wilgen et al. 1996).

- Disease invasion—where the introduction and spread of emergent diseases into wildland plant and animal communities are driven by an array of factors acting individually and synergistically. These include: (1) land use change encroaching on natural areas, such as land conversion for agriculture, settlement, and water impoundment (giving rise, for example, to zoonoses—animal diseases transmitted through contact of wildlife with domestic animals and humans) (Patz et al. 2000), (2) atmospheric N deposition and elevated atmospheric CO_2 (e.g., affecting susceptibility to disease due to altered plant growth patterns) (Mitchell et al. 2003), (3) diminished plant community diversity resulting in increased host-species densities (e.g., directly through management or indirectly through plant preferences of introduced grazers) (Borer et al. 2009), and (4) changing climatic conditions (Crowl et al. 2008; Patz et al. 2000; Woods et al. 2005). Introduction of new diseases and elevated infection rates significantly impact the structure and function of ecosystems (Anderson and May 1986; Crowl et al. 2008), with the outcome determined in interaction with climate and other stressors.

Such a multiple-stressor context provides for a more encompassing assessment of climate vulnerability, yet with concomitant levels of added uncertainty (Sala et al. 2000).

4.0 Implications for Biodiversity Conservation: Fundamentals, Uncertainties, and Planning

4.1 Fundamentals of Vulnerability

Fundamental lessons that emerge regarding the vulnerability of biodiversity to climate are:

- Biodiversity at species through landscape levels is vulnerable to climate acting (1) directly on organisms—which, through ecological networks, generate and are subject to higher-order population, community, and ecosystem vulnerabilities, (2) indirectly through climatic alteration of the physical environment, and (3) synergistically with other stressors.
- At the species level, adaptive capacity—countering such vulnerability—arises from (1) physiological breadth, (2) life-history strategies affecting population viability, (3) flexibility of interspecific (mutualistic, competitive, and trophic) interactions, and (4) dispersal capable of tracking shifting favorable conditions elevationally and laterally.
- Species adaptive capacity is mutable through (1) phenotypic plasticity and (2) microevolution—both highly variable among species as a function of genetic, reproductive, and coevolutionary controls. Some elements of adaptive capacity are latent—potentially released by changing conditions (such as release from competition and triggering of cryptic genetic variation).
- Genetic basis of adaptive capacity geographically varies over a species range as a consequence of (1) variation in microevolutionary potential, (2) abiotic and biotic environmental gradients affecting selective pressure, and (3) climatic and evolutionary history.
- Vulnerability of communities and ecosystem material and energy flows emerges from (1) community composition, especially as it relates to the functional diversity of species (i.e., in terms of general functional types and species with system-determining traits), (2) complexity and strength of interactions, especially the extent to which trophic network structure is

determined by bottom-up and/or top-down interactions, and (3) matter and energy exchange among landscape units (and with domains farther afield).

- In all these aspects, vulnerability is context dependent, for example: what (what species, with what genetics, and in what community networks), where (in the core versus margin of its geographic range, and in what current climatic, physiographic, and ecological region), and when (what history, what foreseeable future threats).

4.2 Uncertainties

These vulnerabilities involve complex interactions among multiple system components and across a broad range of time and space scales. This complexity results in nonlinear dynamics, as previously noted, potentially exhibiting lagged (Jones et al. 2009; Metzger et al. 2009) and threshold (regime-shift or tipping-point) behavior (Barnosky et al. 2012; Biggs et al. 2009; Burkett et al. 2005; Malhi et al. 2009). Such systems are inherently difficult to predict (Hastings and Wysham 2010; Holt 1990; Scheffer et al. 2009; Wardle et al. 2004), affecting our ability to assess species and system vulnerability.

Given that vulnerability is judged relative to the magnitude and nature of stressors, such assessment is also hampered by uncertainty in drivers of change—whether climatic or from other threats, as previously discussed. Predictability is additionally constrained by our limited understanding of even modest portions of vulnerability dynamics summarized in the previous section (and in Figure 1)—especially when focused on a species or community of concern, much less for whole landscapes. One source for this deficiency is insufficient observations of systems under rapid, multisource environmental change that would reveal key dynamics—such as, to name but a few:

- Latent adaptive capacity of species—such as phenotypic plasticity, microevolution, and cryptic genetic variation
- Co-microevolutionary potential of mutualists (e.g., Rice and Emery 2003)
- Cross-temporal and spatial scale population responses to climate variability (e.g., Hallett et al. 2004; Stenseth and Mysterud 2005)
- Role of interspecific competition during species range movement (Davis et al. 1998)
- Threshold versus system-stabilizing community dynamics (e.g., de Ruiter et al. 1995)
- Dynamics leading to the rise of novel ecosystems (Williams and Jackson 2007).

In sum,

- Biodiversity is vulnerable to changing climate conditions across its breadth and depth—that is to say, altering composition, structure, and function of species genetics and populations and communities, ecosystems, and landscapes. Vulnerability is highly interwoven across these levels and across temporal and spatial scales, as well as being context dependent.
- Uncertainty in the outcomes of this vulnerability, however, is high—that is, potentially equal to or greater than the magnitude of the vulnerability.

The bottom line is that the task of incorporating climate vulnerability into conservation planning is both essential and inherently difficult.

4.3 Dealing with Climate Uncertainty in Conservation Planning

While plausible future changes in climate put at risk species persistence and the integrity of community networks and ecosystem function, uncertainty in how this will be played out means we are far from being able to adequately assess 'on the ground' outcomes of this vulnerability. Such uncertainty can be perceived as overwhelming, blocking progress toward including climate vulnerability in conservation planning. To overcome this roadblock, a strategy is needed to deal with uncertainty in an appropriate way—that is, a strategy that explores and copes with uncertainty, rather than putting it aside.

There are many areas in our professional and personal lives where we undertake strategic planning in the context of uncertain future conditions; nonetheless, we face these uncertainties and devise and implement plans according to our expertise and information available. Conservation planning by its nature deals with threats that have highly unpredictable elements such as habitat fragmentation, invasive species, or altered disturbance regime. We may not know, for example, the timing, duration, intensity, location, or other critical attributes of a threat, yet conservation teams devise management plans to address these threats (Groves 2003).

We can also look for guidance for planning under uncertainty in disciplines farther afield. Uncertainty in financial markets has similarities with that in ecological systems (Scheffer et al. 2009). In both cases, high uncertainty arises from:

- Low predictability due to system complexity—e.g., from nonlinear, positive and negative feedback, threshold, and cross-scale (micro- to macroeconomic, genetic to ecosystem) dynamics.
- Poorly understood (and poorly quantified) system-wide behavior or behavior of even limited domains (i.e., economic sectors, 'vulnerability domains' in Figure 1).
- Unknown, or not widely recognized, intrinsic and extrinsic threats to system stability.

We can then borrow basic tenets from financial planning for a scheme for conservation planning under an uncertain climate future. In analogy to 'to invest smart,' 'to conserve smart' is to implement strategies that recognize and handle uncertainty—that hedge against worst-case scenarios, but which do not lead to poor decisions under current conditions. I paraphrase six investment 'coping with uncertainty' tenets which contribute to an integrated conservation strategy for climate change (presented in Section 4.4). (Quoted investment lessons are not from specific sources, but, rather, are common guidance found, for example, on the Internet.)

4.3.1 Tenet 1: Monitoring and Historical Analysis

Monitoring temporal dynamics and long-term trends develops a knowledge base and intuition of system dynamics influencing biodiversity on which to base and modify decisions (analogous to "Never invest in something you don't understand"). An early emphasis on monitoring, if not already ongoing, builds an observational dataset that can be the basis for historical analyses and model development. Initiating monitoring at the onset—not after the planning process is completed nor as an afterthought to monitor a plan's effectiveness—has the benefit of providing the longest possible record. A longer observational record increases the chance of capturing dynamics counter to or more complex than our expectations (e.g., shifting or unstable behavior). Care should be taken in designing and implementing a monitoring program to assure that the record is free from

inhomogeneities and other data quality issues so it may be relied on for temporal analyses (Kittel 2009).

Analysis of long-term records lends valuable insights to the question of vulnerability and with it a first-order estimate of future behavior. However, this tenet comes with a caution regarding extrapolation, that future dynamics may well go outside of what has been observed in the past ("Past performance is no indication of future return").

4.3.2 Tenet 2: Diversify Holdings

A common conservation planning strategy for identifying critical locations for protective measures is to select a portfolio of best sites possible—sites with, for example, (1) the largest populations of a species or the greatest extent of an ecosystem of interest, (2) the best quality of habitat, and (3) the lowest level of threats, current or foreseeable (such as areas with substantial buffer zones—e.g., buffered from roads and other human development). These 'best of the best' criteria assist in selecting conservation sites with the most intact processes supporting biodiversity and ecological and evolutionary function.

Achieving diversity among such sites in terms of their key attributes is a complementary strategy to reduce risk to biodiversity under high environmental uncertainty ("Diversify your portfolio to reduce risk"). Selecting multiple sites under best-site criteria for multiple conservation elements (species and ecosystems) will diversity holdings as a matter of course, with sites selected to optimize criteria in different ways for different elements. However, as in investing, site diversification can adhere to yet higher standards—a diversity of sites meeting best-condition criteria may be akin to a portfolio of highly-rated stock diversified across sectors; focused on stock, it has higher risk relative to one diversified with additional instruments as bonds, real estate, and commodities ("Similarity among holdings reduces a portfolio's effective diversification"). Concepts (and tools) regarding financial portfolio optimization can be employed to design and evaluate diversification in conservation plans (Ando and Hannah 2011; Moore et al. 2010).

An additional strategy to enhance diversity in site selection is to recognize opportunities to support adaptive capacity in otherwise passed-over sites. For example, low priority sites—whether an occurrence of a currently small, unviable population or a marginal habitat—may have greater value in light of climatic uncertainty if they harbor critical source populations for geographic expansion and genetic diversity or have the potential to develop into prime habitat under a more favorable climate. In addition, currently low value, degraded sites with good potential for restoration have added value if they offer an opportunity to re-establish key habitats and landscape integrity, improving species and system adaptive capacity (Johnson et al. 2005; Renton et al. 2012). This is not a strategy to select poor sites per se, but to seek value in less favorable locations.

4.3.3 Tenet 3: Multiple Planning Horizons

Biodiversity conservation planning is by definition for the long-term. However, under a changing but uncertain climate, devising a plan relevant to both current and (indeterminable) future states is problematic. A solution is to develop a multiple-goal conservation plan, where different conservation strategies are developed for different planning horizons ("Establish multiple investment strategies to meet financial goals for different time horizons"). One such multi-goal approach is to focus separately on short- versus long-term climate risk, following a scenario of

climate change shifting from being moderately to severely disruptive to species and ecosystems over the coming decades—a scenario consistent with fundamental lessons regarding plausible climatic change and ecological vulnerability (Sections 2.0 and 4.1). These two planning horizons have their parallels elsewhere in species conservation assessment, such as in 10- and 100-year timeframes used for evaluating population reduction and extinction risk in the International Union for Conservation of Nature Red List (International Union for Conservation of Nature 2010).

Moderate Climatic Disruption Strategy

Under a multiple-time horizon approach, conservation strategies for the near term could consider potential climatic change over, for example, the next 10–20 years to be sufficient to alter population survivorship and landscape processes—but under which species and ecosystems are still capable of local adaptation. Goals would then be to:

- Protect current and restore potentially high-value conservation sites (per Tenet 2)
- Implement measures to protect and enhance species and system adaptive capacity (with respect to climate, other stressors, and their synergisms) and species potential for microevolutionary change.

Corresponding strategies could include:

- Supplementing the list of species and systems of conservation concern with those elements not currently considered at risk but which may become so due to their climate vulnerability (e.g., Horn 2011).
- Preferentially increasing conservation goals (quantity and quality of sites) for species and systems identified as most vulnerable to climate change (e.g., Horn 2011; Howard and Carver 2011).
- Selecting landscape units that increase landscape and regional connectivity and increase buffering from other threats to reduce species and system vulnerability (e.g., Kittel et al. 2011c).

These goals and strategies are consistent with conservation practice employed for other threats (Groves 2003), and so do not rely on any innovation other than to treat climate as an additional threat with its own attributes (Kittel et al. 2011c). Ideally, this is a ‘no regrets’ strategy as it encompasses conservation actions which would have been called for without explicit consideration of climate issues and, by supporting adaptive capacity, has benefits in regard to other threats regardless of whether climate changes substantially or not (Howard et al. 2010; Wilby and Vaughan 2011). These actions are more likely ‘least regrets,’ as opposed to ‘no regrets,’ because of implementation or opportunity costs associated with increases in or some shifting of conservation priorities (Wilby and Vaughan 2011).

Severe-Disruption Strategy

In the longer term, such as over the next 70–100 years, we can consider the possibility that climatic conditions could change so much that there is little expectation that ecosystems would be the same or that any species of concern would be retained locally (Araújo et al. 2004; Bachelet et al. 2001). Such a severe disruption requires that we consider substantially different adaptation strategies and conservation goals (Seastedt et al. 2008).

Given the uncertain status of local and regional biodiversity under this scenario, an approach is to look beyond biological attributes of a landscape and consider how the physical landscape supports biodiversity (without any expectation of what ecosystems may arise there with time) (Kittel et al. 2011a). A strategy is to select landscapes (1) for current physical integrity (with little disruption of, for example, hydrologic network function and soil and geomorphologic processes) and (2) to capture a region's physiographic diversity (e.g., based on elevation, slope, aspect, stream order, lake basin attributes, and bedrock geology). Such landscapes may offer the best prospect for retention of intact ecological and evolutionary processes and for future development of new, functioning ecosystems (Anderson and Ferree 2010; Beier and Brost 2010; Cowling et al. 1999; Kittel et al. 2011a). As 'enduring landscapes,' these physical landscapes are largely defined by their topographic and geologic character and so are generally not sensitive to climate changes at ecological time scales (unless significant changes in geomorphology result from climate shifts, for example).

4.3.4 Tenet 4: Expect surprises—Scenario planning

As noted earlier, species or system vulnerability is relative to the magnitude and nature of a threat. While moderate- and severe-disruption contexts (Tenet 3) give us the opportunity to develop generalized magnitude-linked strategies, we can also employ 'scenario planning' to consider vulnerability under a suite of more specific, qualitatively-distinct alternative future states. Derived from military and business applications for dealing with high uncertainty, conservation scenario planning generates a limited set of 'what if' scenarios selected to reflect the breadth of probable—as well as less probable but still plausible—futures (Peterson et al. 2003). These form alternative reference frames for assessing species and system vulnerabilities on which to base a suite of conservation strategies. This approach can be implemented by a team of experts offering diverse perspectives, drawn from multiple disciplines and professional backgrounds (e.g., from non-governmental organizations, agencies, and research institutions) (Kittel et al. 2011c; MacMillan and Marshall 2006; Peterson et al. 2003; Runge et al. 2011).

In contrast to projections which (1) suggest a probabilistic relationship between altered drivers and outcomes (with the probability usually implied but not known or quantifiable) (MacCracken 2001) and (2) commonly are used in climate impact assessments (e.g., Fischlin et al. 2007), scenarios reflect the possible rather than just the probable and can be the foundation of vulnerability assessments (Kittel et al. 2011c; Peterson et al. 2003). Scenarios can be general or specific statements of contrasting future states and can be developed from observed system behavior, system sensitivity from model projections, and 'imaginative speculation'—the last is to challenge our thinking about future dynamics beyond those experienced or expected (Peterson et al. 2003; Turner et al. 2003) (an example application in conservation planning is given in: Horn 2011; Howard and Carver 2011; Kittel et al. 2011c).

4.3.5 Tenet 5: Save Aggressively and Early

If uncertainty is so large that site diversity, multiple time horizon, and scenario planning strategies (Tenets 2–4) seem insufficient, the fallback hedge against uncertainty is to implement conservation action more extensively across the landscape ("Save aggressively to counter downside risk"). An example would be to have greater redundancy in the number of sites fulfilling any one goal. This would likely expand conservation site selection into lower priority, low quality areas (e.g., Kittel et

al. 2011c) and might call for restoration to realize the potential adaptive capacity of these landscapes. As with any conservation plan, a complementary strategy is to implement its components as soon as feasible given that opportunity costs (lost opportunities) for protecting habitats and landscapes increase with time, as key environments are degraded by other stressors ("Start investing early"); this need is only intensified with climatic uncertainty (Hannah et al. 2007).

In conservation planning, the question of "How much is enough?" is one difficult to address (1) because of uncertainty in future levels of risk from both known and unanticipated threats and (2) because, for more pragmatic considerations, conservation plans often call for a level of action greater than feasible given limited opportunity and financial resources. That said, high uncertainty in climate risk ups the level of critical conservation action needed to reduce the vulnerability of species and ecosystems and should provide additional incentive for action by agencies, conservation organizations, and other public and private stakeholders.

4.3.6 Tenet 6: Revisit Goals and Strategies—Adaptive Management

A conservation plan for reducing climate vulnerability needs to include a review process for keeping the plan on goal by incorporating monitoring feedback and new information ("Periodically reevaluate financial goals, adjust investment strategies accordingly"). This is to help cope with uncertainties in how conservation strategies will play out due to (1) unexpected species and system dynamics and (2) unanticipated changes in external forcings (including from new threats).

One approach for on-going reassessment in conservation planning is 'adaptive management' (Keith et al. 2011). Adaptive management is an iterative process of (1) reassessing species and system status through monitoring, (2) evaluating current and alternative innovative strategies through research and expert elicitation, and (3) adapting conservation plans in light of these new insights (Conroy et al. 2011; Runge et al. 2011; Williams et al. 2007). The adaptive process could include periodic reappraisal of goals, vulnerability assessments, and strategies to take into consideration:

- Observed changes to populations, communities, and ecosystems—including those tied to conservation plan achievements and failures to date.
- Increased understanding of external forcing and internal dynamics.
- New opportunities—such as from new ideas, tools, stakeholders, and government policies.

4.4 A Vulnerability Approach for Conservation Planning

Consideration of climate in conservation planning often takes the form of impact assessments, where the goal reflects a perceived need to determine specifics of how, where, and which elements of biodiversity might be strongly altered under rapid climate change. Explicitly driven by climate projections, this approach is referred to as 'top down' as it follows the progression of cause and effect. However, this requires skillful prediction and a certainty in future forcings—which, in all practicality, are not achievable (Sections 2.1.2 and 4.2). Consequently, high uncertainty and low predictability limit the value of model projections for conservation planning. Such limitations include that: (1) spatial and temporal details in projections are not definitive enough to be relied on for planning, even when downscaled, (2) the use of ensembles of projections to capture a range of outcomes still constrains our outlook, as they (most likely) underrepresent a larger domain of possible futures that may arise from unforeseen or poorly modeled forcings and dynamics, and (3) projections do not necessarily capture critical attributes of climate relevant to understanding

ecological, hydrological, and other terrestrial and aquatic processes (such as key variables at appropriate timescales) (Kittel et al. 2011c).

Alternatively, if we acknowledge that high uncertainty in future outlooks cannot be sufficiently reduced, it may be more productive to rephrase our goal to one of decreasing the vulnerability of species and systems (Dawson et al. 2011; Kittel et al. 2011c). This 'vulnerability approach' focuses on enhancing adaptive capacity as a means to lower or cope with risks from uncertainties (Pielke et al. 2012; Turner et al. 2003). In contrast to projection-driven assessments, this is a 'bottom-up' approach as it looks to understand species and ecosystem dynamics that determine their vulnerability (Pielke et al. 2012). This approach focuses on producing planning outcomes that better recognize and handle uncertainties, employing strategies that do not rely on the temporal and geographic details of model projections (Kittel et al. 2011c).

In the vulnerability approach, the investment-analog tenets (Section 4.3) give us a framework for handling uncertainty in a 'smart' (appropriate) manner while devising strategies to support the adaptive capacity of species and systems. Stemming from these tenets, planning decisions are facilitated by the integration of expert knowledge, scenario planning, a no-regrets goal, and adaptive management as follows:

- Expert synthesis of established knowledge provides an opportunity to gain insights into the resistance and resilience of species and systems to a changing climate and, based on this, to devise strategies to reduce or cope with this risk (Dawson et al. 2011) (see also: Comer et al. 2012; Game et al. 2011; Hannah et al. 2002b; Hansen et al. 2010; Mawdsley et al. 2009).
- Scenario planning gives us the means to not rely on climate and ecological model projections for systems whose complexities are, as already described, inherently difficult to simulate; rather, scenario planning gives us a framework with which to envision consequences to biodiversity across a broad spectrum of plausible futures (including conceivable 'surprises').
- A no-regrets goal guides us to implement climate-adaptive strategies which benefit current conservation needs by also decreasing species and system vulnerabilities to the suite of other threats.
- Adaptive management protocols give conservation programs the flexibility to adjust strategies to changing conditions and advances in our understanding.

The broader the perspective and more integrative the expert synthesis is in its consideration of fundamental determinants of biodiversity's vulnerability to climate the better. This calls for a suite of short-term and long-term (multiple planning horizon) climate adaptive measures to sustain or restore (1) population viability, dispersal, and microevolutionary processes, (2) trophic, competitive, and mutualistic community networks, (3) landscape disturbance regimes, and (4) ecosystem energy and material flows. The resulting design is to support, at least for the near-term, existing patterns of compositional, structural, and functional biodiversity and, in the longer term, to allow for their potential reconfiguration on the landscape as climatic conditions shift.

Such strategies can be devised and deployed using current best conservation practices, including those for maintenance and reestablishment of the physical and biological integrity of the environment, along with reduction of direct and synergistic effects of other threats. Also derived from the tenets for coping with climatic uncertainty, strategic options include diversification,

restoration, enhancement of buffering and connectivity, ‘enduring landscape’ conservation, and ‘save more/save early’ actions.

This process is clearly inexact, limited by our understanding of species and system adaptive capacity (Section 3.0) and inherent constraints on environmental predictability. Given the essential yet difficult task of conservation planning in light of biodiversity’s vulnerability to climate change, the vulnerability approach, integrated with strategies to handle uncertainty, offers a path for us to prepare, even if reluctantly, for an uncertain ecological future.

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Illustrations

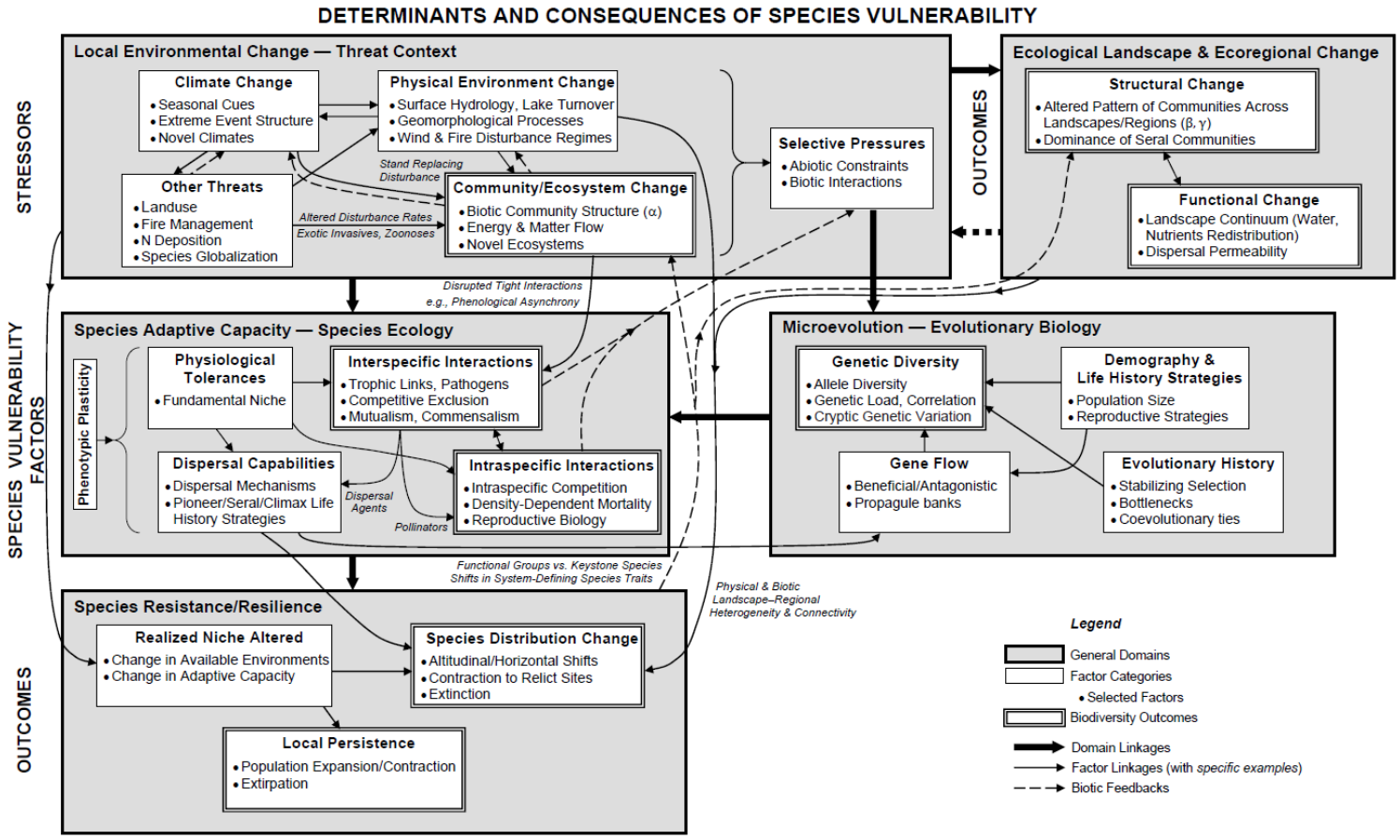

Figure 1. Determinants and consequences of species vulnerability. The figure is broadly organized into domains of stressors (climate and other anthropogenic environmental changes, *top left panel)*, species-level vulnerability factors (which limit or support a species' adaptive capacity, *middle panels*), and outcomes. Factors that set a species' vulnerability are its current adaptive capacity (*middle left panel*) and microevolutionary shifts in this capacity (*middle right panel*). Outcomes of these vulnerabilities include species persistence and range changes (*bottom panel*), altered landscape and regional ecological heterogeneity (*top right panel*), and changes to genetic diversity, community structure, and the complexity of ecosystem interactions—all of which are elements of biodiversity (double-bordered boxes). Selected factors (bulleted items) give examples for factor categories, and factor linkages and feedbacks (narrow-lined arrows) illustrate interactions; not all possible factors and linkages are shown. With respect to local and regional/landscape community structure, symbols α, β, and γ refer to Whittaker's (1960) levels of species diversity, where α = site (sample) species diversity, γ = regional total diversity, and β = among-sample heterogeneity in species diversity across the region.

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