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Abstract: The impacts on biodiversity and ecosystems are among the key reasons for concern about climate change. Integrated assessment models are the main tools used to estimate the global economic benefits of policies that would address climate change, but these models typically include only a partial accounting and idiosyncratic treatment of ecosystem impacts. This report reviews several recent studies of the impacts of climate change on biodiversity. We also review recent quantitative estimates of the rate of species extinctions, the impact of climate change on biodiversity, and the value of biodiversity loss. Based on these estimates, we re-calibrate the biodiversity loss function in the FUND integrated assessment model, and we develop a new global biodiversity nonuse value function. These could serve as replacements for the functions currently used in FUND, or as a preliminary ecosystem damage function in a new integrated assessment model. We also highlight areas where further research is needed for developing more comprehensive and reliable forecasts of ecosystem damages as a result of climate change.

Keywords: climate change, ecosystem, biodiversity, integrated assessment model, structural benefit transfer

Subject areas: 28, 45, 62

JEL codes: Q51, Q54, Q57

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1 Introduction -

The impacts on biodiversity and ecosystems are among the key reasons for concern about climate change (Smith *et al*. 2009). Integrated assessment models (IAMs) are the main tools used to estimate the global economic benefits of policies that would address climate change (Kelly and Kolstad 2000), but these models include only a partial accounting and idiosyncratic treatment of ecosystem impacts. In this report we review recent research on the potential impacts of global warming on biodiversity, and we develop a modified biodiversity value function that could be used in a simplified global integrated assessment model of climate change. We also highlight areas where further research is needed for developing more comprehensive and reliable forecasts of ecosystem damages as a result of climate change.

The report is structured as follows. In Section 2 we review the projected impacts of climate change on ecosystems. We focus mainly on global species loss and draw heavily on the IPCC reports and several more recent studies. The main aims of this section are to describe the key mechanisms by which climate change is expected to impact biodiversity, briefly explain the approaches that ecologists used to examine the potential effects of climate changes on species, and summarize the range of projected impacts that can be found in the literature. In Section 3 we discuss the ecosystem damage estimates in three simple integrated assessment models of climate change: PAGE, DICE, and FUND. The limited representation of ecosystem damages in these models is understandable in light of the relatively sparse research on people's willingness to pay for biodiversity protection at the global scale. However, it stands in contrast to the growing body of scientific studies that point to potentially severe impacts on biodiversity and ecosystems (Pereira *et al*. 2010). In Section 4 we examine the ecosystem damage function in FUND and update some of its key parameters based on more recent research. We also develop a new biodiversity nonuse value function that could serve as a replacement for the ecosystem damage function currently used in FUND or in other simple IAMs. We conclude in Section 5 with a brief summary and discussion of areas where more research is needed.

2 Impacts of climate change on ecosystems

Since the establishment of the Intergovernmental Panel on Climate Change (IPCC) in 1998, changing climatic conditions have been tracked in many locations across the earth. Part of the impetus for these observations is to record the effects of climate change on wildlife and ecosystems. The view of most natural scientists who closely study these issues is that climate change has already begun to impact natural systems, often by disrupting the evolved structure of local biological communities and by exacerbating the demands of human populations on the provision of ecosystem goods and services (Diaz *et* al. 2006, Parmesan 2006, IPCC 2007). Such goods and services represent the return on natural capital assets for human economies, as summarized in the Millennium Ecosystem Assessment (MEA 2005a). In the coming century, climate change is expected to become an increasingly important driver of ecosystem and biodiversity modifications throughout the world, with great potential to further disrupt ecosystem functioning and impact the availability of natural capital for human use (Sala *et al.* 2000).

The IPCC's Fourth Assessment Report identified several direct and indirect impacts of climate change on biodiversity and ecosystem processes. Much of the research in this area has focused on impacts at the level of species' populations, and a variety of morphological, physiological, behavioral, and reproductive changes in plant and animal populations have been linked to climate change (e.g., Hughes 2000, Walther *et al.* 2002, Parmesan 2006). More recent studies have examined the impacts of climate change on evolutionary processes and genetic changes in populations (e.g., Thomas *et al.* 2001, Thomas 2005, Bradshaw and Holzapfel 2006). A growing body of research has implicated climate change in species- and community-level changes, as well. Among the most commonly cited impacts are geographical shifts in species distributions and abundances (Parmesan *et al.* 1999, Grabherr *et al.* 2001, Thomas *et al.* 2001, Walther *et al*. 2005). Additionally, changes in phenology—the timing of life-cycle processes such as migration, plant bud break, winter hibernation, etc.—have been correlated with local temperature increases for many taxa (Menzel and Estrella 2001, Parmesan and Yohe 2003, Root *et al.* 2003, Root and Hughes 2005). Climate change also has been found to alter the composition of biological communities through local extinctions and invasions (Walther 2000, Walther *et al.* 2002, Thomas *et al.* 2006) and can impact communities via altered biotic interactions including predator-prey relationships, mutualistic interactions, and disease and parasite dynamics, among others (Kerr and Kharouba 2007).

The IPCC's Fourth Assessment Report indicated a likely global average surface warming of 1.1-6.4°C by the end of this century relative to average temperatures between 1980 and 1999. Thus, understanding the impact of temperature increases on patterns of biodiversity is of fundamental importance to quantifying the ecological and economic risks of climate change. The remainder of this section reviews recent projections of species' responses to temperature changes. At the outset we note that most research to date in this area has focused on the impact of climate change on species range sizes and extinction risks, with very little quantitative research on the subsequent impacts of species movements and extinctions on ecosystem functions and services. This is a gap in the literature that we will not fill in this report—we merely highlight it as an important area for future research. In the meantime, we will develop a new value function that is designed to capture only the "nonuse" value of global biodiversity loss. In the language of the Millennium Ecosystem Assessment, this includes some of the "cultural services" of ecosystems and the "supporting services" that would underpin these, but excludes "provisioning" and "regulating" ecosystem services. The "use" values that arise through species' contributions to these other classes of ecosystem services would need to be assessed separately.

Before reviewing recent studies of the impacts of climate change on biodiversity, we take a step back to very briefly review estimates of "natural" (or "historical") and "current background" species extinction rates. The natural extinction rate excludes recent human causes of extinction, such as habitat destruction and over-harvesting, and can be estimated from the fossil record. The current background extinction rate includes species losses due to both natural and human causes, but for our purposes we specifically exclude extinctions brought about by climate change. These distinctions are important because in a later section we will develop a biodiversity value function where the value of species losses will depend on the level of biodiversity. Thus, valuing the loss of biodiversity from climate change (or any other specific cause) will require projecting the overall loss of biodiversity over time, not just the loss as a result of climate change per se.

Natural rates of species extinctions as estimated from the fossil record are believed to be in the range of 10^{-7} to 10^{-6} extinctions per species per year—i.e., the average time between speciation and extinction is on the order of 1 to 10 million years—and are generally considered to be relatively stable over geologic time (May *et al*. 1995). Several attempts have been made to estimate the current background rate of species extinctions—including both natural causes and anthropogenic causes such as habitat destruction—with mixed results. May *et al*. (1995) estimated the current background extinction rate to be roughly 10^{-3} extinctions per species per year. Pimm *et al*. (1995) estimated the current background extinction rate to be in the range of 2×10^{-5} to 2×10^{-4} extinctions per species per year. However, Pimm *et al*. also noted that if all threatened species were to become extinct within 100 years the current background rate could be as high as 1.5×10^{-3} extinctions per species per year, which is in rough agreement with the estimate of May *et al*. (1995).

2.1 Species responses to climate change

Predictions of species' responses to future climate changes are highly uncertain for at least three reasons. First, the factors that influence the diversity and geographic distribution of species across Earth are still not fully understood (Allen *et al.* 2002). Explaining the abundance and distribution of species over space and time is a fundamental task of ecology, but it has proven extremely difficult to characterize the precise mechanisms by which the current global arrangement of species has come to exist. Indeed, ecological rules governing the assembly of communities of species or predicting the abundance of species in a given region are few (Roughgarden 2009). Several new general theoretical frameworks for ecology have been proposed in recent years (e.g., Hubbell 2001, Brown *et al.* 2004, Ritchie 2009, Loreau 2010), but it still seems doubtful that a single "unified theory of biodiversity" will emerge in the near future. Until then, the predictions scientists are able to make about species' responses to climate change will necessarily be limited by our currently incomplete understanding of the mechanisms that underlie the historic and current distribution of species (Kerr and Kharouba 2007).

Second, while projections of future average global surface temperatures are relatively robust, there remains a great deal of uncertainty regarding future climate conditions at regional and local scales. Climate change will vary across regions, and therefore will impact the biota of some regions more than others. For example, with respect to temperature increases, it is expected that terrestrial areas will warm more than the oceans, and that the polar and temperate latitudes will warm more than the tropics (IPCC 2007). Moreover, because individuals, populations, and communities of species will interact with climatic changes at local, rather than regional or global scales, the roughly continental-scale projections of temperature increases currently available may not be sufficiently precise for analyzing species' responses to climate change. Moreover, there is significant heterogeneity among the leading climate models regarding their predicted changes in moisture and precipitation. The interactions between temperature and precipitation regimes can have profound effects on the types of organisms that can survive in a location, so having reliable information for only one of these parameters may be an insufficient basis for accurately predicting species responses.

Finally, different species may react very differently to increasing temperatures based on their unique physiological tolerances, migration abilities, population structure, and genetic variability, among other factors (Davis and Shaw 2001, Kerr and Kharouba 2007). If so, then individual species—rather than communities of organisms or ecosystems—should be the focal point of these investigations. However, analyzing and interpreting the responses of millions of different species is untenable, especially considering the lack of detailed knowledge about the current patterns of global biodiversity, individual species characteristics, and geographic ranges. The use of the relatively few species in regions for which we have adequate data to serve as representatives of the far more numerous set of still-unstudied species may impart unknown biases that further cloud the interpretation of extrapolated global biodiversity responses to climate change.[1] Nonetheless, models of species' responses to climate change still can be informative and may be useful for indicating the plausible range and relative likelihoods of potential outcomes. In any case, they are the best tools currently available for the task. Over time, we would expect these models to be improved as new observations of ecological changes accumulate and provide data for comparison to prior model predictions.

Though many uncertainties remain, a framework for understanding species' responses to climate change has emerged from the developing field of global change ecology. As the effects of climate change will vary over different locales, different populations of each species will be affected by varying conditions. In some locales, the effects of climate change may be slight; some organisms in these locales may be able to tolerate new environmental conditions with minimal impact on their physiological states and overall rates of reproduction and survival. This tolerance to changing conditions is referred to as "phenotypic plasticity," the varied capability of individuals to adopt morphological, physiological, or behavioral changes during their lifetime in direct response to changing environmental conditions (Chevin *et al.* 2010). However, populations with limited phenotypic plasticity or that reside in areas with more dramatic climate changes will not be able to simply tolerate the environmental changes in their locales. The net result of these population responses to varied climate impacts across a species' range is manifested in the species' response to climate change. Ultimately, species, as aggregated populations of similar organisms, will react to increasing global temperatures with three potential responses: adaptation, migration, or extinction—with the first two of these not necessarily mutually exclusive. Most research to date has focused on range adjustments due to migration and extinction as species' primary responses to temperature increases.

2.1.1 Adaptation

Adaptation is the evolutionary ability of a population to become better suited to its environment. For populations exposed to increased temperatures, adaptation would involve changes in the behavioral, physiological, and/or structural aspects of organisms

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[1] If errors in temperature predictions are uncorrelated with species' sensitivities to climate change, and if the likelihoods of local extinctions are approximately linear over the relevant range of temperature changes, then the errors in predicting species extinctions at local scales may be offsetting when summed to produce predictions of biodiversity loss at larger scales. However, these are two big "ifs" about which we can only speculate.

that better allow them to thrive in a warmer environment (Thomas 2005). However, adaptations require many generations to arise and increase in frequency within a population. One consequence of this is that large organisms with long generation times are much less likely than small organisms with shorter generations to evolve adaptive responses to climate change. A common view is that climate changes are occurring too quickly for adaptation to play a significant role in saving many populations from extinction in areas where new climate conditions will exceed the physiological tolerances of the local biota (e.g., Kerr and Kharouba 2007). However, this is still an open question and an active area of research as some recent studies suggests that the ability for organisms to respond to climate change, including via adaptation, may be severely underestimated (e.g., Willis and Bhagwat 2009).

2.1.2 Migration

Many species that avoid extinction may do so by means of latitudinal or elevational migrations. Migration is the movement of individuals and populations leading to species range expansions or contractions. Because lower latitudes are the richest areas in terms of number of species—possibly in part due to higher average temperatures and, therefore, higher net primary productivity—the expansion of warmer climates may promote increased species richness at higher latitudes. Recent evidence suggests that some species already have begun expanding their range into higher latitudes and elevations to track shifting temperatures (Parmesan *et al.* 1999, Walther *et al.* 2002, Hughes *et al.* 2003, Kerr and Kharouba 2007).

However, species are limited in their ability to track climate changes via migration because of their inherent dispersal capabilities (Malcolm *et al.* 2002, Svenning and Skov 2004, Kerr and Kharouba 2007). Most species are sedentary, with local colonizations and extinctions among sub-populations of larger meta-populations driving species range adjustments rather than long-range individual movements (Parmesan *et al.* 1999). Nevertheless, even among these sedentary species, relative dispersal abilities can make the difference between species survival and extinction. For many species, poleward colonizations may not occur quickly enough to offset the effects of extinctions in the lower latitudes of their range, potentially leading to species collapse (Malcolm *et al*. 2002).

In addition, habitat fragmentation can greatly diminish the effective migration potential of populations to track their ideal climate conditions in human-modified landscapes (e.g., Collingham and Huntley 2000, Thomas 2000, Hill *et al.* 2001, Warren *et al.* 2001, Travis 2003, Bomhard *et al.* 2005, Kerr and Kharouba 2007). In the extreme, fragmentation of habitats can create physically impassable barriers to some species. Even for species that are able to move between fragmented suitable patches, their reproductive capacities and genetic variability may be eroded by reduced population densities (Da Fonseca *et al.* 2005).

2.1.3 Adaptation & Migration

Understanding the interplay between simultaneous or alternating adaptation and migration responses to climate change is a relatively recent area of study in climate change ecology. Nevertheless, some evidence suggests that recent evolutionary changes in the dispersal abilities of species can be linked to climate changes (Davis and Shaw 2001, Hughes *et al.* 2003, Thomas 2005). These dispersal adaptations may come at the expense of investment in other traits including reproductive output (Hughes *et al.* 2003). Such evolutionary trade-offs will affect range expansion rates and patterns, which may ultimately determine the success or failure of species to cope with climate change (Hughes *et al.* 2003). Further research on the potential interactions of these responses to climate change is needed (Thomas 2005, Kerr and Kharouba 2007).

2.1.4 Extinction

Populations that cannot adapt to or migrate with changing climatic conditions will be unable to survive. These localized species extinctions can be detrimental to ecological communities and to the delivery of ecosystem services to human populations in afflicted regions (Hooper *et al.* 2005, Kerr and Kharouba 2007). Species with small ranges or narrow climatic tolerances are at the highest risk of extinction because they are likely to have fewer and less dense populations in a smaller geographic area (Kerr and Kharouba 2007). If temperature regimes increase too much and too rapidly across a species' entire range, which is more likely for species with small ranges, all populations that comprise the species may be threatened. In contrast, species with large ranges or broad climatic tolerances will likely maintain some populations that are mildly or not at all threatened, and thus, even though some populations may be extirpated, the species as a whole will survive (Kerr and Kharouba 2007).

2.2 Projections of species loss due to climate change

Two recent studies have examined the potential loss of species diversity caused by climate change at the global scale. First, Thomas *et al*. (2004a) combined the results of six previous studies that used "climate envelope modeling" to predict the effects of climate change on species extinction rates. Climate envelope modeling uses the "association between current climates (such as temperature, precipitation and seasonality) and present-day species distributions to estimate current distributional areas. The 'climate envelope' represents the conditions under which populations of a species currently persist in the face of competitors and natural enemies" (Thomas *et al*. 2004a p 145). Thomas *et al.* used a species-area relationship (SAR) to translate the outputs of the primary studies, each of which predicted the change in the range size of regional suites of species in a warmer climate, into projections of overall species losses in such climates.

A species-area relationship (SAR) takes the form $S = cA^z$, where *S* is the number of species inhabiting an area of size *A*. Ecologists have found that the exponent *z* lies in the range of 0.15-0.25 under a wide variety of circumstances (with lower values associated with continuous or "continental" habitats and landscapes and higher values with discrete or "island" habitats and landscapes), but the leading coefficient *c* is highly variable and depends on the scale of observation (Gould 1979). However, only the exponent *z* is needed for predicting proportional changes in species numbers due to habitat loss as represented by changes in *A*. Specifically, the fraction of species lost, L, if the area is reduced from A_1 to A_2 is $L = 1-\left(A_2 / A_1\right)^z$.

Based on a variety of sensitivity analyses, including three different CO_2 scenarios and three alternative applications of the SAR, Thomas *et al*. (2004a) estimated that 9-52% of species may be "committed to extinction" by 2050.[2] Under the most rapid climate change scenario examined, with atmospheric CO_2 concentrations exceeding 550ppm by 2050, Thomas *et al.'s* (2004a) extinction estimates ranged from 21% to 52%, with a scenario mean of 35%.

Several limitations of the methods used by Thomas *et al*. (2004a) have been identified by other researchers, including their unconventional use of species-area relationships (Buckley and Roughgarden 2004, Harte *et al.* 2004, Lewis 2006), potential biases inherent in the primary studies used in their meta-analysis (species pools consisting of mostly endemic or small-range species) (Lewis 2006), and the potentially inconsistent combination of disparate bioclimatic envelope models from the primary studies (Thuiller *et al.* 2004). In response to these and other comments, Thomas *et al.* (2004b) noted that model differences accounted for a much smaller portion of the uncertainties in their projected extinction risks than their dispersal and climate change scenarios. However,

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[2] Thomas *et al*. used the SAR, with *z* = 0.25, to synthesize the results of many species-level projections of changes in range sizes, indexed by $i = 1,2,...,n$, in three different ways: 1). $L = 1-\left(\sum_{i=1}^{n} A_{2,i} \Big/ \sum_{i=1}^{n} A_{1,i}\right)^z$, 2.) $L = 1-\left[(1/n)\sum_{i=1}^{n}\left(A_{2,i}/A_{1,i}\right)\right]^z$, and 3.) $L = (1/n)\sum_{i=1}^{n}\left[1-\left(A_{2,i}/A_{1,i}\right)^z\right]$. In all cases, if A_2 was greater than A_1, Thomas *et al*. assumed $L = 0$ (i.e., no loss or gain of species).

subsequent research also has shown that alternative bioclimatic envelope models can produce highly divergent projections of the magnitude and direction of species range shifts caused by climate change (Araujo *et al.* 2005a, Araujo *et al.* 2005b). Bioclimatic envelopes tend to underestimate the true range of climate variation tolerable for each species (Araujo & Pearson 2005) while assuming that current species distributions are in equilibrium with their climate tolerances, and discounting biotic factors such as predation, competition, host availability, among others (Peterson *et al.* 2005). Furthermore, these models may overestimate habitat loss and extinctions because they are unable to capture the fine-scale geographical, topological, and climate variation that might exist in the form of microrefugia and the ability for species to acclimate and exploit secondary habitats (Willis & Bhagwat 2009, Pereira *et al.* 2010). For example, a recent study suggests that many tree species were able to survive previous glacial maxima as widespread, low-density populations in geographic areas previously thought intolerable under glaciation-event climate regimes (McLachlan *et al.* 2005). This ability of species to maintain low-density isolated populations for long periods of time while the regional "average" climate is unsuitable provides a fundamental challenge to projecting future impacts on biodiversity with bioclimatic envelope models (Pearson 2006). Therefore, at its current stage of development, the main value of bioclimatic envelope modeling may lie in providing a useful first approximation of the broad patterns of future impacts rather than accurate simulations of the future distributions of particular species (Pearson and Dawson 2003). As a result, it may be misleading to use these projections for direct predictions of risk (Araujo *et al.* 2005a, Araujo and Rahbek 2006).

Another study of projected global species losses as a result of future climate change was conducted by Malcolm *et al.* (2006). Malcolm *et al.* (2006) used two dynamic global vegetation models (DGVMs) and seven general circulation models (GCMs) to project changes in the distribution of major biome types and associated extinctions of endemic plant and vertebrate species in 25 current biodiversity hotspots under a climate scenario with a doubling of CO_2 in 100 years. Changes in the modeled spatial extent of vegetation communities or biomes were used as proxies for changes in available habitat. Malcolm *et al*. (2006) examined the sensitivity of their results to multiple models of biome categorization, species' biome specificity, migration abilities, and the specific DGVM used to simulate biome cover changes. To help account for small-ranged species biases they used an "endemic-area relationship" (EAR), which counts only those species that are unique to the study area, rather than all species that occur in the study area as in the traditional SAR (see Kinzig and Harte 2000; but also see Ulrich 2005). The authors also sought to control for the effects of anthropogenic habitat fragmentation by using an exponent $z = 0.15$ in the EAR (in contrast to Thomas *et al.'s* use of $z = 0.25$ in the SAR). Malcolm *et al.* estimated that between <1% and 43% of species would be threatened with extinction under a scenario with doubled atmospheric CO_2 concentration by 2100, with an overall mean estimate of 11.6%.

Dynamic Global Vegetation Modeling has been criticized as problematic for predictions of species extinctions because they model responses of species communities to climate change. Malcolm *et al*. (2006) themselves acknowledge that individual species, rather than communities, will respond to climate change. Future biomes may or may not resemble current biomes—perhaps just organized in new geographical arrangements—and it is unclear how much biodiversity might be retained within novel biomes should they arise. Furthermore, the predicted species extinction rates are highly sensitive to several model assumptions that are difficult to verify. For example, assumptions regarding species' biome-specificity greatly influence the results of the study, with nearly two times or greater importance than the DGVM used, migration ability assumed, or the biome classification scheme (Malcolm *et al.* 2006).

Despite the limitations highlighted above, and the likelihood that realized extinction rates will be lower than "committed to extinction" rates (Pereira *et al.* 2010), the projections of Thomas *et al*. (2004a) and Malcolm *et al*. (2006) represent the best currently available predictions of the effects of global warming on global species richness. However, the total number of species is only one aspect of the broader concept of "biodiversity," and not necessarily the most important index to use when monitoring biodiversity losses or evaluating the performance of conservation strategies. In addition to the knowledge gaps highlighted in the preceding sections, additional research is needed on alternative indices of biodiversity for use in studies of ecosystem services and the economic values of those services.

2.3 Implications for ecosystem services

The relationships between biodiversity, ecosystem functioning, and the maintenance of ecosystem goods and services is a growing focus of inquiry among ecologists and other environmental and social scientists (Hooper *et al.* 2005, MEA 2005a, Diaz *et al.* 2006). Species losses may diminish the availability of ecosystem goods and services through changes in ecosystem structures and functions (NRC 1999, MEA 2005a, MEA 2005b). However, the cumulative changes in ecosystems brought about by species turnover, migrations, and the development of novel communities may be more significant to the provision of ecosystem goods and services than species extinctions. The ability for these processes to augment or further constrain the diversity and supply of these goods and services is another research area of urgent need if we are to accurately predict the impacts of climate change on biodiversity and human well-being. Ecosystem services have been linked to human well-being through a variety of direct and indirect channels, so the accelerated degradation of ecosystem service flows could have important economic and social consequences (MEA 2005a). However, our understanding of the relationships between ecosystem services and human well-being is far from complete, so more research is still needed in this area (Raudsepp-Hearne *et al*. 2010).

Ecosystem changes and the associated impacts on human settlements and economies are mostly absent from economic integrated assessment models (IAMs) of climate change due, in part, to a lack of reliable quantitative estimates. Climate change may affect a wide variety of ecosystem goods and services, such as pest control, pollination, seed dispersal, decomposition and soil maintenance, subsistence hunting, outdoor recreation, ecotourism, cultural and religious symbols, and more (IPCC 2001 p 276-278). Because many of these goods and services have indirect-use and nonuse (existence) values, they are difficult to quantify using traditional economic valuation methods (Freeman 2003 p 457-460). In the next section, we review the treatment of ecosystem damages in three of the most widely used IAMs in the climate economics literature.

3 Ecosystem damages in integrated assessment models

There are many integrated assessment models designed to examine climate change, but only a subset of these focus on the economic damages from climate change impacts at a global scale. Three of the most prominent IAMs in this category are PAGE, DICE, and FUND. These models are designed to estimate the aggregated economic damages of climate change impacts at a global scale over a long time horizon, 200 years or more, so they are necessarily highly simplified in many respects. Moreover, there is wide variation in the detail with which different categories of climate change damages are represented in these models. A good overview of each of these models and some of their key ingredients is provided by Mastrandrea (2009). In this section we examine whether and how ecosystem damages are represented in PAGE, DICE, and FUND. This will serve as a jumping off point for the following section, where we develop a new biodiversity value function that could be included in these or other IAMs.

3.1 PAGE

The "Policy Analysis of the Greenhouse Effect" (PAGE) model is designed to "allow all five of the IPCC's reasons for concern [including 'risks to unique and threatened ecosystems'] to be captured in an integrated assessment framework" (Hope 2006). PAGE includes separate damage functions for two broad sectors, "market" and "nonmarket," in each of eight world regions. The damage functions include a "tolerable" level of temperature change below which no damages occur, which can be increased over time by adaptation. The damage functions also include the risk of "possible future large-scale discontinuities," which would cause damages equivalent to 5% to 10% of GDP, depending on the region. No detailed discussion of the representation of ecosystem damages is provided in the model documentation (Hope 2006, 2008), so it is not possible to determine what portion of the total damages are attributable to impacts on biodiversity or other ecological functions or structures. This also means that it is not clear how the damage functions in PAGE could be modified to incorporate new research on ecosystem impacts and values, short of a wholesale re-calibration of all damage categories simultaneously.

3.2 DICE

The "Dynamic Integrated Climate Economy" (DICE) model is based on globally aggregated Cobb-Douglas production function and a representative agent who chooses the level of investment and greenhouse gas abatement in each period to maximize the discounted flow of future utility from consumption. Abatement is costly, but it allows the agent to reduce climate change damages, which are represented by an aggregate damage function that is calibrated to match the sum of damages to a variety of sectors including agriculture, health, and ecosystems and settlements, among others, as estimated in a collection of previous studies (Nordhaus and Boyer 2000). DICE uses a series of subjective judgments to represent the potential impacts of global warming on ecosystems:

> "This set of issues reflects a wide variety of factors that are difficult to model and quantify but may be of major concern… Given the lack of any comprehensive estimates, the authors have made rough estimates here of the extent to which the economy and other institutions are vulnerable to climate change… it is assumed that the capital value of climate-sensitive human settlements and natural ecosystems range from 5 to 25 percent of regional output; for the United States, this number is estimated to be 10 percent of national output… we assume that each subregion has an annual willingness to pay 1 percent of the capital value of the vulnerable system (which is one-fifth of the annualized value at a discount rate on goods of 5 percent per year) to prevent climate disruption associated with a 2.5˚C rise in mean temperature… It must be emphasized that this methodology at this stage is speculative…" (Nordhaus and Boyer 2000 p 85-87).

This means that the value of impacts on "human settlements and natural ecosystems" from climate disruption associated with a 2.5˚C rise in mean temperature is assumed to be equivalent to one percent of ten percent (i.e., 0.1%) of the value of global economic output. The value of total damages from a 2.5˚C rise in mean temperature in DICE2007 is 1.74% of global economic output, so the percent of total damages attributed to impacts on "human settlements and natural ecosystems" is 0.1% ÷ 1.74%, or 5.7%.

3.3 FUND

Among the three IAMs reviewed here, the "Framework for Uncertainty, Negotiation, and Distribution" (FUND) model (Tol 2002a,b) includes the most detailed representation of multiple categories of potential climate change damages, including an explicit damage function pertaining to ecosystem impacts. In Section 4.2 we give the functional forms that comprise the FUND ecosystem damage function, so in this section we simply document the origins of this function as described by the model developers. Anthoff and Tol (2008) describe the ecosystem damage function in FUND as follows:

> …the impact of climate change on ecosystems, biodiversity, species, landscape *et cetera* [is assessed] based on the 'warm-glow' effect. Essentially, the value, which people are assumed to place on such impacts, are indepent of any real change in ecosystems, of the location and time of the presumed change, *et cetera*—although the probability of detection of impacts by the 'general public' is increasing in the rate of warming.

Tol (2002a) gives a more detailed discussion:

> The impact of climate change on species, ecosystems and landscapes is here assessed based on the following four assumptions:
>
> - Climate change is unambiguously perceived as bad. Although impacts vary between species, systems, places and time, this assumption reflects that people tend to be conservative (i.e., any change is bad) and that negative impacts tend to attract more attention than positive ones.
> - The actual change does not matter, the fact that something has changed does. This reflects the "warm-glow"-effect in the literature… Although contested, the warm-glow effect suggests that people's willingness to pay reflects their desire to contribute to a vaguely described "good cause," rather than to a well-defined environmental good or service. The impact of climate change on nature will be diffuse, hard to measure, and hard to distinguish from other changes. The value is set at an average of $50 per person in the OECD (Pearce 1993).
> - The figures of Pearce (1993) reflect a willingness to pay to preserve through direct action. It is assumed that the willingness to pay to preserve through indirect action (greenhouse gas emissiosn abatement), and the willingness to accept compensation for a loss have the same $50 value.
> - Lastly, the OECD value for 1990 has to be transferred to other regions and other times.

4 An updated ecosystem damages function -

The ecosystem damages function in FUND3.3 consists of two parts: a biodiversity loss function, which relates temperature changes to the rate of species extinctions over time, and a biodiversity value function, which relates the decline of global species richness to willingness to pay.[3] We will retain this basic two-part structure, but we will re-calibrate the parameters of the biodiversity loss function and we will develop an alternative biodiversity value function and calibrate its parameters.

4.1 Biodiversity loss function

The biodiversity loss function in FUND3.3 is highly simplified. It is designed to forecast the change in the stock of "biodiversity"—specifically, species richness—at the global scale over time. The dynamics of the global stock of biodiversity (i.e., species richness), B_t, are ascribed to two factors: a background rate of biodiversity loss, θ, which is independent of climate change and is assumed constant, and an additional rate of loss due to climate change, which is assumed to be proportional to the square of the year-to-year change in temperature, $\varphi \Delta T_t^2$. Specifically, the biodiversity loss function in FUND3.3 is:

$$B_{t+1} = B_t \left(1 - \theta - \varphi \Delta T_t^2\right). \qquad (1)$$

The simplicity of this function—in particular, its scalar nature—is its main weakness, since it cannot hope to represent the full spatial and taxonomic heterogeneity of biodiversity in all its forms. At the same time, its simplicity also is its main strength, since it is sufficiently parsimonious to be calibrated using the few relevant quantitative studies available from the literature, as reviewed above in Section 2.2.

The parameter values used in FUND3.3 are $\theta = 0.003$ (with a range of 0.001 to 0.005) and $\varphi = 1.6$ (with a range of 0 to 3.2), and the initial level of biodiversity in 2000 is assumed to be 14 million species.[4] These figures are described as "expert guesses" (Anthoff and Tol 2008 p 11-12).

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[3] To be specific, the FUND3.3 model documentation refers to "economic damages." These are denominated in money units, but no precise economic value interpretation is given. When any questions arise in this regard, we assume that "economic damages" refers to the current consumption-equivalent compensating variation of the associated climate impacts.

[4] The original formulation of the biodiversity loss function in FUND3.3 also includes a lower bound on biodiversity equal to 1% of the current stock. We ignore this feature here since it seems unnecessary. Also,

As reviewed in Section 2 above, estimates of the current background rate of biodiversity loss are around 10^{-3} (May *et al*. 1995, Pimm 1995), and we adopt this value here. To calibrate φ, we use results from the studies by Thomas *et al*. (2004b) and Malcolm *et al*. (2006), which were described in Section 2.2 above. Specifically, we relate the biodiversity loss function in FUND3.3 to the results of these studies as follows:

$$1-L=\frac{B'_H}{B_H}=\frac{B_0\left[1-\theta-\varphi\Delta T^2\right]^H}{B_0\left(1-\theta\right)^H}=\left[\left(1-\theta-\varphi\Delta T^2\right)\big/\left(1-\theta\right)\right]^H, \tag{2}$$

where L is the fraction of species "committed to extinction" or "threatened by extinction" by some future year H, B'_H is the estimated level of biodiversity in year H under a constant annual temperature change scenario, B_H is the estimated level of biodiversity in year H if the temperature does not change over this time span, B_0 is the initial level of biodiversity, ΔT is the constant annual temperature change up to year H, and the other parameters are as defined above. Solving for φ, the parameter in FUND that we are trying to calibrate, gives:

$$\varphi=\left\{\left(1-\theta\right)\left[1-\left(1-L\right)^{1/H}\right]\right\}\big/\Delta T^2 . \tag{3}$$

Table 1 includes three scenarios extracted from both Thomas *et al*. and Malcolm *et al*. and the calibrated values for φ based on each scenario according to equation (3). The calibrated values based on the scenarios reported by Thomas *et al*. are roughly 1.5 to 4 times larger than the FUND3.3 default central value of φ = 1.6. The calibrated values based on the results of Malcolm *et al*. span a much wider range, from a low value that is more than an order of magnitude smaller than the FUND3.3 default value to a high value that is roughly 50% greater than the FUND3.3 default value. The differences among the results of these studies and the full range of estimates from both studies highlights the uncertainty regarding future species losses due to climate change. It may be possible to narrow this range further by more closely examining these and possibly other studies, but we leave this for future work. For the illustrative calculations in this paper, we use the value of φ that minimizes the sum of squared errors between the log of the L's predicted by equation (2) and the log of the L's reported by the two studies listed in Table 1 using their associated

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in FUND3.3 the parameter φ is comprised of two separately defined parameters, $\varphi=\gamma/\tau^2$, but here we lump them into a single quantity to streamline the calibration.

values for ΔT and H and θ = 10^{-3}, which gives φ = 1.21.[5] This is somewhat lower but reasonably close to the central estimate in FUND3.3, which is 1.6.

4.2 Biodiversity value function

The ecosystem damages function in FUND3.3 can be written as

$$d_{tr} = \left\{ \alpha \left(\omega^{-1} + \psi \omega^{-2} \right) \right\} \frac{y_{tr}}{1 + \psi / y_{tr}} \left(\frac{\Delta T_{tr} / \tau}{1 + \Delta T_{tr} / \tau} \right) \left[1 + \sigma \left(\frac{B_0 - B_t}{B_t} \right) \right], \tag{4}$$

where d_{tr} is the per capita economic damage (which we interpret as the willingness to pay to avoid the loss of global biodiversity due to climate change) in year *t* for a representative resident of region *r*, y_{tr} is average per capita income in year t and region r, ΔT_{tr} is the temperature change between year $t-1$ and t in region r, and B_t is the level of global biodiversity in year *t*. The central parameter values used in FUND3.3 are α = 50, ω = 24,401, ψ = 30,000 [1995$/person/yr], τ = 0.025 °C, σ = 0.05, and B_0 = 14,000,000.

A qualitative explanation of the rationale for this functional form was provided by Tol (2002a) and Anthoff and Tol (2008), as reviewed in Section 3.3 above. However, we are not able to infer a utility-theoretic foundation for this function based on direct inspection of its structure and the description of the authors, and at least two features of this function seem counterintuitive. First, there is a component of the damages that depends only on the temperature change, not the level of biodiversity: even if $B_t = B_0 \ \forall t$ in equation (4), ecosystem damages are still positive if $\Delta T_{tr} > 0$. Furthermore, as we show below, this component comprises a large majority of the damage. Second, there are no damages if the year-to-year temperature change is zero. Even if the temperature anomaly is positive and large, and—more importantly—even if the level of biodiversity is rapidly shrinking, damages are calculated to be zero if the temperature does not change from one year to the next.

In this section we develop an alternative damage (specifically, willingness-to-pay) function that does not have these features. Later we will compare the damage estimates from the FUND3.3 ecosystem damage function to those from our alternative damage function, which will further highlight these points.

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[5] Minimizing the sum of squared errors between the (unlogged) L's reported by Thomas *et al.* and Malcom *et al.* and those predicted using equation (2) gives φ = 1.17.

Our alternative value function is based on a representative individual who aims to maximize the discounted sum of her and her heirs' utility. She assumes that the household size of her heirs will not change, i.e., births will balance deaths over time. Time is discrete, and the individual discounts her own and her heirs' period utility at a fixed pure rate of time preference, ρ. We will assume that household consumption of market goods and services is proportional to income in every period, and that the marginal utility of consumption diminishes at a constant relative rate, η. We further assume that the individual attaches a value to biodiversity that is additively separable from income (consumption of market goods and services) in the period utility function,[6] and the marginal utility of species-weighted biodiversity is inversely proportional to its level. Specifically, the individual has a well-defined ranking of species from highest to lowest value where the weights decline exponentially with the species rank. Putting all of this together, we can write the representative individual's value function as

$$V = \sum_{t=0}^{\infty} \left[{y_t}^{1-\eta} / (1-\eta) + \beta \ln\left(\sum_{k=1}^{B_0} \lambda e^{-\lambda k} p_{tk} \right) \right] e^{-\rho t} , \tag{5}$$

where y_t is the individual's income in period *t*, *k* indexes the species ranks, λ is the rate at which the value weights decline with species rank, B_0 is the initial global species richness, and p_{tk} is the probability that species of rank *k* is not extinct in period *t*. The expected value of a sum of independent random variables is the sum of the expected values of its components. In this case the components are the probabilities that each individual species is still extant at some future date, each a 0-1 variable. So, assuming species' fates are independent, the sum of these probabilities is the expected total number of extant species at that date, which means that expected biodiversity in period *t* is $B_t = \sum_{k=1}^{B_0} p_{tk}$.

We will we set $\eta = 2$ and $\rho = 0.01$, which are middle-of-the-road values for these preference parameters from the climate change economics literature (Newbold *et al.*

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[6] The strong separability between consumption and biodiversity in the utility function means that we are focusing here on the pure "nonuse value" of biodiversity, in the sense of Freeman (2003 Ch 5), since changes in the level of biodiversity (through this channel of the utility function) would have no influence on the individual's consumption of market goods and services. In a typical integrated assessment model in the mold of PAGE, DICE, or FUND, the "use value" of biodiversity—i.e., the provisioning, regulating, and some of the cultural ecosystem services that are provided or supported by biodiversity (MEA 2005a)—would be represented through functional dependencies between the output of various market sectors (such as agriculture and fisheries) and nonmarket sectors (such as outdoor recreation) and one or more ecosystem flows or stocks, which could include species richness among other ecological endpoints.

2010).[7] The remaining preference parameters to be calibrated are β and λ. We will make use of two biodiversity valuation studies to calibrate these parameters. In the end, only β will play a role in our ecosystem damage function (since only B_t will be included as an argument, not the p_{tk}'s), but λ will be needed to make use of the second of the two biodiversity valuation studies that we will use to calibrate β.

First, we consider the study by Kramer and Mercer (1997), hereafter "K&M," who used a stated preference survey to estimate U.S. citizen's willingness to pay to protect tropical rainforests. The respondents were told that 5% of rainforests were currently protected, and that protecting an additional 5% would be sufficient to reach a policy goal recommended by experts. K&M presented two estimates (based on two alternative econometric specifications) of the average lump sum willingness to pay to protect an additional 5% (110 million acres) of all rainforests: $33 and $48 per household (converted from 1992$ to 2010$ using the consumer price index).

We will link K&M's central estimates of willingness to pay to the value function for our representative individual in two stages. First, we will make a series of assumptions about the survey respondents' "mental model" of the relationships between rainforests, biodiversity, and biodiversity loss over time.[8] Then we will derive an expression for the individual's lump sum willingness to pay in the first period for a decline in the rate of global biodiversity loss.

For the first stage, we assume that the respondents made a specific set of functional and quantitative assumptions about rainforests, biodiversity, and biodiversity loss over time. The functional assumptions are that biodiversity outside and inside of rainforests can

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[7] Jacobson and Hanley (2009) estimated that the income elasticity of WTP for biodiversity protection is less than one. In our model this elasticity will be close to η.

[8] A completely separate but also highly speculative set of simplifying assumptions will be required to link the second study (by Richardson and Loomis 2009) to our biodiversity value function later in this section. That we find ourselves in a position where we must try to peer into the heads of the respondents to make the necessary links between the results of these stated preference studies and our value function highlights the thinness of the body of available evidence in the environmental economics literature on people's willingness to pay for the protection of global biodiversity. So, while we freely admit the highly conjectural status of this exercise, we will press on under the assumptions that: 1.) the mere process of explicitly laying out the full chain simplifying assumptions necessary to support the transfer of these study results to our biodiversity value function will help to highlight some of the key gaps in the literature that must be filled before an improved biodiversity value function can be developed, 2.) the exercise may serve as an illustrative example of the "preference calibration" or "structural benefits transfer" valuation approach (Smith *et al.* 1999, 2006), and 3.) even the rough-and-ready parameter estimates we are able to derive here may still be a useful supplement to the models that are currently available.

be represented by two additively separable species-area relationships, each with a common exponent but with possibly different coefficients, and non-rainforest habitat is assumed to remain intact but rainforest habitat is subject to a constant rate of loss over the foreseeable future. The quantitative assumptions are that tropical rainforest comprise 10% of all terrestrial habitats,[9] 50% of all terrestrial biodiversity is contained in tropical rainforests,[10] the species-area exponent is 0.25 (a common estimate, which also matches the value used by Thomas *et al*. (2004a)), the baseline rate of rainforest habitat loss is 0.9% per year (Kramer *et al*. 1995 p 6), and that currently 5% of rainforests are protected (as indicated to the survey respondents in the questionnaire used by Kramer *et al*. 1995). Putting these assumptions together, the forecasts of biodiversity under the baseline and hypothetical scenarios are

$$B_t = c_A A_0^{\,z} + c_R\left(PR_0 + (1-P)R_0 e^{-\delta t}\right)^z$$

and (6)

$$B_t + \Delta B_t = c_A A_0^{\,z} + c_R\left((P+Q)R_0 + (1-P-Q)R_0 e^{-\delta t}\right)^z,$$

where c_A and c_R are the species-area coefficients for non-rainforest and rainforest habitats, A_0 and R_0 are the current areas of non-rainforest and rainforest habitats, δ is the rate of habitat loss, z is the species-area exponent, P is the currently protected fraction of rainforests, and Q is the additional fraction protected under the hypothetical scenario of the stated preference survey. In the nomenclature of these equations (6), our specific quantitative assumptions are: $c_A A_0^{\,z} / c_R R_0^{\,z} = 1$,[11] $z = 0.25$, $\delta = 0.009$, $P = 0.05$, and $Q = 0.05$. Next, dividing the second equation in (6) by the first, then plugging our specific quantitative assumptions into the resulting expression, we can derive the following equation for the relative difference in biodiversity between the baseline and hypothetical scenarios in all future years:

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[9] Kramer *et al*. (1995) indicated that "…36 percent of the tropics is covered by natural forests, an area amounting to about 1,715 million [1.175×10^9] hectares" (p 6). The surface area of Earth is 5.1×10^{10} ha, one third of which is covered by land.

[10] http://www.scientificamerican.com/article.cfm?id=earth-talks-daily-destruction

[11] This is the symbolic version of our assumption that 50% of all terrestrial species reside in tropical rainforests: the numerator is the number of terrestrial species outside of rainforests, and the denominator is the number of species inside rainforests.

$$\frac{\Delta B_t}{B_t} = \frac{1+\left[P+Q+(1-P-Q)e^{-\delta t}\right]^z}{1+\left[P+(1-P)e^{-\delta t}\right]^z} - 1. \tag{7}$$

Our assumptions imply that global biodiversity under the hypothetical scenario, with an additional 5% of tropical rainforests protected, will be roughly 0.74%, 1.8%, and 3.3% higher than under the baseline scenario in 100, 200, and 300 years, respectively. This is the increase in biodiversity over time for which we assume the K&M survey respondents (implicitly) understood that they were being asked to pay.

Next we must derive an expression for willingness to pay in the first period for a decrease in the rate of biodiversity loss over time. To do this, we suppose that the survey respondents assumed that species' future survival probabilities are essentially uncorrelated with their value ranks, and that the value ranks are uncorrelated with habitat types.[12] That is, the respondents viewed the loss of tropical rainforests as a threat to global species diversity per se, not necessarily to particular named species for which they may have special concerns. In this case, $\sum_{k=1}^{B_0} \lambda e^{-\lambda k} p_{tk} = \left(\sum_{k=1}^{B_0} \lambda e^{-\lambda k}\right) \times \left(\sum_{k=1}^{B_0} p_{tk}\right)$. Normalizing the species weights, the first summation in this product, such that they sum to 1, the period utility function simplifies to $y_t^{1-\eta}/(1-\eta)+\beta \ln B_t$. This means that only β is estimable using the K&M results. Modifying equation (5) accordingly, and then setting the baseline value equal to that with increased biodiversity in all future periods, ΔB_t, less a lump sum payment in the first period, WTP, allows us to solve for the one-time willingness to pay:

$$WTP = y_0 - \left[y_0^{1-\eta} + \beta(\eta-1)\sum_{t=0}^{\infty} \ln(1+\Delta B_t/B_t)e^{-\rho t}\right]^{1/(1-\eta)}. \tag{8}$$

Equation (8) can be solved for β to directly calibrate the value of this parameter corresponding to the estimates of willingness to pay reported by K&M. We set y_0 equal to the median household income of the survey respondents, which was \$48,950 yr^{-1} (converted from 1992\$ to 2010\$ using the consumer price index). The calibrated values for β using the two alternative estimates of average willingness to pay reported by K&M

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[12] Some support for these simplifying assumptions can be found in the results of Martin-Lopez *et al.* (2008), who conducted a meta-analysis of 60 species valuation studies. They found no strong evidence of a relationship between people's willingness to pay for species protection and the species' degree of endangerment (as assessed by the IUCN), and they found that willingness to pay was not statistically different among taxonomic groups or ecosystems.

are shown in the first two rows of numbers in Table 2. To help put these estimates in context, the final two columns of the table show the implied lump sum willingness to pay to prevent global biodiversity from decreasing by 5% and 50% in all future periods relative to their projected levels associated with each calibrated value of β.

Next we turn to the study by Richardson and Loomis (2009), hereafter "R&L." These authors conducted a meta-analysis of 31 stated preference studies published between 1983 and 2001 designed to estimate the willingness to pay to protect a variety of endangered and threatened species. We assume that the survey respondents understood the hypothetical scenarios to imply that the focal species in the survey was "committed to extinction" under status quo conditions and that the hypothetical species protection program they were being asked to consider would reduce the species' risk of extinction down to the average background risk of extinction faced by all other species. With these simplifying assumptions, the lump sum willingness to pay to protect species *k* is

$$WTP_k = y_0 - \left[y_0^{1-\eta} + \beta\left(\left(1-\eta\right)/\rho\right)\ln\left(1-\lambda e^{-\lambda k}\right)\right]^{1/(1-\eta)}. \tag{9}$$

The lowest estimate of lump sum willingness to pay to prevent a species from extinction reported by R&L was $22 (for the arctic grayling), and the highest was $380 (for the bald eagle) (where both figures have been adjusted from 2006$ to 2010$ using the consumer price index). To link these estimates to the willingness-to-pay given by expression (9), we assume that these species correspond to two specific ranks in the average respondent's species value ordering. Considering that most stated preference studies of willingness to pay for species protection focus on either highly charismatic species or otherwise locally important species, we assume that the lowest valued species in the R&L meta-dataset lies somewhere between the 10th and 200th rank, and the highest valued species lies somewhere between the 1st to 20th rank. These are arbitrary endpoints, but we assume that they are sufficiently wide to cover most of the range of plausible values. The next five rows of Table 2 show the calibrated values of β and λ for five pairs of assumed species rankings of the lowest and highest valued species in the R&L meta-dataset.

The calibrated values for β using the R&L study are all within one order of magnitude of each other, and the two calibrated values for β using the K&M study fall within the range of values calibrated using the R&L results. To choose a single point value for β, we use the pair of preference parameters [β, λ] that minimize the sum of squared errors between the logs of the WTP estimates reported by K&M and R&L in the second column of Table 2 and the logs of the associated WTP's predicted using equations (8) and

(9) using the assumed species ranks listed in the third column, which gives $\beta = 9.5\times10^{-8}$ and $\lambda = 0.015$.

The overlap in the β estimates in Table 2 shows a surprising degree of consistency considering the large differences in the nature of these two economic valuation studies. K&L valued the protection of natural habitat that serves as a storehouse of biodiversity in a faraway region, and R&L conducted a meta-analysis of studies that valued the protection of particular species that were likely very familiar to the survey respondents. Nevertheless, we view these calibration results as preliminary rather than definitive and we view our calibrated point value for β as a placeholder only. We also believe the paucity of biodiversity value estimates in the environmental economics literature reflected here emphasizes the need for additional research to synthesize the existing economic valuation studies of biodiversity loss and to conduct new studies to fill the gaps in the literature.

4.3 Comparison to FUND3.3

In the meantime, with all parameter values specified we now can compare the forecasts of our ecosystem damage function to FUND3.3. To do this, we use both functions to calculate incremental damages for a representative household over the next 150 years under a scenario where the global average surface temperature increases by 0.025 deg C each year relative to a counterfactual scenario with no temperature change. Specifically, we use equation (4) to calculate the incremental damages in each year in the FUND model. To calculate a measure of damages in each year that is directly analogous to the damages, d_t, calculated by the FUND3.3 ecosystem damage function in equation (4), we calculate willingness to pay in each year, wtp_t, based on our value function in equation (5):

$$wtp_t = y_t - \left[y_t^{1-\eta} + \beta(\eta-1)\ln\left(1+\Delta B_t/B_t\right)\right]^{1/(1-\eta)}. \tag{10}$$

This is the amount of income that the representative individual would be willing to pay in year *t* to have biodiversity at level $B_t + \Delta B_t$ rather than B_t. For both functions we assume that the representative individual has an income of $30,000 in the first year, and her (and her heirs') income grows by 2% per year over the course of the forecast horizon.

Figure 1 shows the baseline biodiversity loss projection assuming no temperature change, the projection under the constant annual temperature change scenario described above using the central parameters values used in FUND3.3, and the projection for the same temperature change scenario using our re-calibrated value for φ as described in Section 4.1. The re-calibrated equation of motion for biodiversity, equation (1), projects a cumulative loss of biodiversity due to climate change—that is, an additional loss above that attributed to non-climate related causes—over this time frame that is roughly 25% less than the cumulative loss projected using the FUND3.3 parameter values. Therefore, our review of the literature on the influence of climate change on the rate of global biodiversity loss is largely consistent with the central parameter values in FUND3.3.

Figure 2 shows the projected damages calculated using the FUND3.3 ecosystem damage function and the projected willingness to pay using the alternative value function based on equation (10) in each of the next 150 years, as a fraction of income in each year. In this figure, both damage functions use the re-calibrated equation of motion for biodiversity, and the FUND3.3 damage function also uses the associated projection of constant annual temperature changes. The solid red line is the FUND3.3 projection of damages, and the solid black line is the projection of willingness to pay using our alternative value function. Both functions project that damages as a fraction of income will increase over time, but FUND3.3 projects this fraction to increase at a decreasing rate while our alternative value function projection increases at an increasing rate.

The behavior of the FUND3.3 projection of damages can be understood by direct inspection of equation (4). We are examining a scenario where the growth rate of income is constant, so eventually y_{tr} (income) will become large relative to the parameter ψ,[13] and, as we will see below, the change in B_t per se makes a very small quantitative contribution to the damages in FUND3.3. Therefore, d_{tr} will eventually grow at the same rate as y_{tr}. (Another way to see this is to note that the elasticity of damages with respect to income is $\frac{1+2\psi/y}{1+\psi/y}$, so as income grows this elasticity approaches one from above.)

On the other hand, under our alternative damage function the growth rate of damages is persistently greater than the growth rate of income. We can understand this behavior by noting that the marginal value of biodiversity in year t is $\beta y_t^{\eta}/B_t$, which grows at the rate $\eta\hat{y}_t - \hat{B}_t$, where the hat's indicate growth rates of the associated variables. Income, y_t, is growing over time (at a constant rate of 2% per year in this example, by assumption) while biodiversity, B_t, is shrinking, so the marginal value of biodiversity will grow faster than η (in this case 2) times the rate of income growth. On top of this, the difference in the level of biodiversity between the two scenarios that we are

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[13] The parameter ψ can be interpreted as the level of income at which damages as a fraction of income, d_{tr}/y_{tr}, equals one half of its maximum value, holding all other variables in the damage function constant.

valuing, ΔB_t, also is increasing over time, so the annual damages, wtp_t—roughly, the marginal value times ΔB_t—will grow even faster.

Finally, note that the dashed red line in Figure 2—just below the solid red line—is the component of the FUND3.3 damages that depends on the temperature change alone, calculated by setting $B_t = B_0 \ \forall t$ in equation (4). This shows that only a very small fraction of the total ecosystem damages in FUND3.3—the narrow wedge between the solid and dashed red lines—arise from biodiversity loss per se. We are unsure how to interpret this feature of the model or if this is what was intended by the model developers, so we merely highlight this result as another point of comparison between the FUND3.3 ecosystem damage function and our alternative damage function, which directly depends on biodiversity loss and only indirectly on the temperature change through its effect on biodiversity.

5 Summary and conclusions

In this report we have reviewed recent studies of the impacts of climate change on biodiversity. The current rate of global biodiversity loss may be two or three orders of magnitude higher than the historical rate, as estimated from the fossil record, and two recent studies suggest that climate change may further increase the current rate of loss by another one or two orders of magnitude. Based on these estimates, we re-calibrated the biodiversity loss function in the FUND integrated assessment model. We also developed a new global biodiversity nonuse value function, and we calibrated its parameters using two non-market valuation studies that examined United States residents' willingness to pay for the protection of tropical rainforests and threatened and endangered species.

When comparting our results to FUND, we find two main differences between FUND's original and our re-calibrated ecosystem damage function. First, when incorporating contemporary scientific projections of biodiversity losses attributable to climate change, our re-calibrated function predicts somewhat lower rate of biodiversity losses over time due to climate change than those predicted in FUND3.3 (Figure 1). Second, our re-calibrated function implies that damages will grow faster than income over time, whereas FUND3.3 projects that damages will grow at the same rate as income over time (Figure 2). As a result, our ecosystem damage function predicts smaller damages in the near-term and much larger damages over the long-term than FUND3.3.

To conclude the report, we briefly discuss some of the major research gaps that must be filled in order to develop more satisfactory models for forecasting biodiversity loss due to climate change, consequent changes in ecosystem services, and people's willingness to pay to avoid those losses. We can loosely categorize these gaps into ecological and economic research priorities.

5.1 Ecological research priorities

The IPCC's Fourth Assessment Report (IPCC 2007) provides a useful summary of the most important gaps in ecologists' abilities to forecast the ecosystem-level impacts of climate change. The areas that were highlighted by the IPCC as high priorities for further research include: (1) ecosystem tolerance and resilence to climate change, (2) links between biodiversity and ecosystem functioning, (3) links between temporal and spatial scales of ecosystem responses, (4) the relationship between biodiversity and resilience of ecosystem services at scales relevant to human well-being, (5) time lags by which productivity and the provision of goods and services by ecosystems respond to climate change, and (6) potential for synergistic and antagonistic effects of climate change and anthropogenic stresses on ecosystems.

Virtually none of the items on this list are explicitly represented in any of the three integrated assessment models reviewed in Section 3 above. Only the FUND model includes an explicit representation of the effect of climate change on ecosystems, and this is limited to the effect of changes in global average surface temperatures on global species richness. Our re-calibration of the parameters of the biodiversity loss function in FUND represents an initial attempt to update the model based on more recent studies, but it should be clear that this is still a very incomplete proxy for a complex category of impacts. Perhaps the most pressing ecological research priority for the purposes of improving integrated assessments of climate change policies is further study of the links between biodiversity and the provision of ecosystem goods and services. The value function developed in this report is most plausibly interpreted as capturing only the nonuse or existence value of global species richness. This leaves all of the direct and indirect use values—i.e., many of the provisioning, regulating, and supporting ecosystem services—of biodiversity still un-quantified.

An even more basic ecological research priority is the continued cataloging and mapping of life in all its forms. This is essential for the continued improvement in forecasting the effects of climate change on biodiversity and ecosystems. These data inform our estimates of the current level and patterns of biodiversity and the current rate of species extinctions, and they form the basis of statistical or mechanistic models designed to predict species' responses to climate changes over time.

Additionally, our re-calibration of FUND's biodiversity loss function relies on estimated rates of historical species extinctions. Specifically, we defined θ as the constant background extinction rate, independent of climate change. However, it is likely that many past extinctions were caused by intermittent changes in climate or other relatively short term environmental changes, so the actual background extinction rate may vary substantially over time. It may be possible to improve our understanding of the role climate change plays in species extinctions, including how the rate of climate change relates to the rate of species extinctions, if the paleological record can be decomposed into time periods associated with known changes in climate or other conditions. In the meantime, it should be understood that the constant background extinction "hazard rate," θ, used here is a simplification mainly intended to distinguish extinctions caused by anthropogenic climate changes, represented by φ, and extinctions due to other non-anthropogenic causes.

In a more theoretical vein, the mechanisms by which phenotypic plasticity, adaptation, and migration can impact the survival of populations and species are also important emerging areas of research that will inform our projections of species losses. A better understanding of these and other evolutionary and ecological processes that combine to determine the abundance and patterns of species over space and time will be crucial in making projections of species declines in the face of future climate changes that will necessarily involve extrapolations far outside of the sample data. And lastly, although not directly an ecological problem, the accuracy and confidence of precipitation projections under different scenarios of atmospheric CO_2 levels must match that of temperature projections in order to assess the nature of climate change at local scales relevant to the plant and animal populations affected.

5.2 Economic research priorities

In Section 4.2 we developed a generic willingness-to-pay function for the protection of global biodiversity. This required the use of a highly simplified functional form with only two free parameters. With the function specified just so, its parameters could be calibrated using two economic valuation studies, one that valued the protection of tropical rainforests, which serve as a storehouse for a disproportionate share of Earth's biodiversity, and one that valued the protection of threatened and endangered species in the United States. We emphasize again that the primary purpose of this exercise was illustrative and that the resulting calibrated parameter values should be considered highly preliminary. They may be suitable for provisional use in simplified integrated assessment models such as those discussed in Section 3—that is, depending on the analysts' and decision-makers' tolerances for model and parameter uncertainties—but we believe that additional research on people's willingness to pay for biodiversity protection is sorely needed before significant improvements can be made in the representation of ecosystem damages in IAMs.

For the specific purposes of improving integrated assessment models, additional research may be most useful if it is divided along two parallel tracks. First, more scientific research is needed to develop climate-response functions that link changes in a set of relevant climate variables to the abundance and distribution of species, and ecological production functions that link the abundances and distributions of species to the provision of valuable ecosystem services such as enhanced productivity of agricultural crops, opportunities for commercial harvesting and recreational hunting or wildlife viewing, the provision of pharmaceutical products, and so on. The economic value of this class of ecosystem services then could be estimated using a variety of revealed preference economic valuation methods, such as production function approaches, hedonic property value models, and recreation demand models (National Research Council 2005 p 100-119). Second, and on a parallel track, more economic research is needed to better estimate the nonuse values of biodiversity protection, which were the focus of our structural benefit transfer exercise above. This category includes all of the intangible values that people attach to species and ecosystems irrespective of any direct or indirect use that they may make of those species now or in the future.

The rationale for this parallel-track research strategy is that stated preference (SP) methods are necessary for estimating nonuse values, since by definition these values leave no behavioral trail that can be exploited by revealed preference (RP) methods, but at the same time SP methods are not well-suited on their own for valuing the many direct and indirect use values of species and ecosystems. Providing reliable responses regarding such use values may require a more sophisticated understanding of the ecological production functions that link species to the provision of tangible ecosystem services than will be understood by, or that can be effectively conveyed to, most respondents in the context of a typical stated preference survey (Boyd and Krupnick 2009). So while SP methods can in principle estimate the total (use + nonuse) economic value of biodiversity, if naively applied in this way they may produce highly imprecise and likely inaccurate estimates.

This suggested division of labor between revealed and stated preference valuation studies in this area of research will involve its own challenges. In particular, it would require stated preference study designers to construct plausible hypothetical scenarios that can effectively isolate the nonuse component of people's value for biodiversity protection. Many stated preference researchers caution against trying to isolate nonuse values, since this may be very difficult to do in practice. However, this difficulty must be set against the disadvantages of using SP studies to try to estimate the total economic value of biodiversity, including the use values of very unfamiliar ecological structures and functions about which most respondents know very little. So two central tasks for researchers who aim to develop better methods for valuing biodiversity and ecosystem services will be to strike the best possible balance between these competing advantages and disadvantages of revealed and stated preference methods, and to further develop and refine the supplemental tools for benefit transfer that will be needed to synthesize the findings of these separate revealed and stated preference studies in such a way that is comprehensive yet avoids double-counting.

References

Allen AP, Brown JH, Gillooly JF. 2002. Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science* 297:1545-1548.

Anthoff D, Tol RSJ. 2008. The Climate Framework for Uncertainty, Negotiation and distribution (FUND), technical description, version 3.3.

Araujo MB, Rahbek C. 2006. How does climate affect biodiversity? *Science* 313:1396-1397.

Araujo MB, Pearson RG. 2005. Equilibrium of species' distributions with climate. *Ecography* 28:693-695.

Araujo MB, Pearson RG, Thuiller W, Erhard M. 2005a. Validation of species-climate impact models under climate change. *Global Change Biology* 11:1504-1513.

Araujo MB, Whittaker RJ, Ladle RJ, Erhard M. 2005b. Reducing uncertainty in projections of extinction risk from climate change. *Global Ecology & Biogeography* 14:529-538.

Bomhard B, Richardson DM, Donaldson JS, Hughes GO, Midgley GF, Raimondo DC, Rebelo AG, Rouget M, Thuiller W. 2005. Potential impacts of future land use and climate change on the Red List status of the Proteaceae in the Cape Floristic Region, South Africa. *Global Change Biology* 11:1452-1468.

Bradshaw WE, Holzapfel CE. 2006. Evolutionary response to rapid climate change. *Science* 312:1477:1478.

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB. 2004. Toward a metabolic theory of ecology. *Ecology* 85(7):1771-1789.

Buckley LB, Roughgarden J. 2004. Biodiversity conservation: effects of changes in climate and land use. *Nature* 430:145-148.

Chevin L-M, Lande R, Mace GM. 2010. Adaptation, plasticity, and extinction in changing environment: towards a predictive theory. *PLoS Biology* 8(4):e1000357.

Collingham YC, Huntley B. 2000. Impacts of habitat fragmentation and patch size upon migration rates. *Ecological Applications* 10:131-144.

Da Fonseca GAB, Sechrest W, Oglethorpe J. 2005. Managing the matrix. *In* Lovejoy TE, Hannah L, eds. *Climate Change and Biodiversity*, p 346-358. New Haven, CT: Yale University Press.

Davis MB, Shaw RG. 2001. Range shifts and adaptive responses to Quaternary climate change. *Science* 292:673-679.

Diaz S, Fargione J, Chapin FS, Tilman D. 2006. Biodiversity loss threatens human well-being. *PLoS Biology* 4:1300-1305.

Freeman AM, III. 2003. *The Measurement of Environmental and Resource Values: Theory and Methods.* Washington, DC: Resources for the Future.

Grabherr G, Gottfried M, Pauli H. 2001. Long-term monitoring of mountain plants in the Alps. *In* Burga CA, Kratochwil A, eds. *Biomonitoring: General and Applied Aspects on Regional and Global Scales—Tasks for Vegetation Science*, p 153-177. Dordrecht, Netherlands: Kluwer Academic.

Gould SJ. 1979. An allometric interpretation of species-area curves: the meaning of the coefficient. *The American Naturalist* 114:335-343.

Hampe A, Petit RJ, Cortufo F. 2005. Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters* 8:461-467.

Harte J, Ostling A, Green JL, Kinzig A. 2004. Biodiversity conservation: climate change and extinction risk. *Nature* 430. DOI: 10.1038/*nature*02718.

Hill JK, Collingham YC, Thomas CD, Blakeley DS, Fox R, Moss D, Huntley B. 2001. Impacts of landscape structure on butterfly range expansion. *Ecology Letters* 4:313-321.

Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setala H, Symstad AJ, Vandermeer J, Wardle DA. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75: 3-35.

Hope C. 2006. The marginal impact o fCO2 from PAGE2002: an integrated assessment model incorporating the IPCC's five reasons for concern. *The Integrated Assessment Journal* 6(1):19-56.

Hope C. 2008. Optimal carbon emissions and the social cost of carbon over time under uncertainty. *The Integrated Assessment Journal* 8(1):107-122.

Hubbell SP. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.

Hughes CL. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15:56-61.

Hughes CL, Hill JK, Dytham C. 2003. Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. *Proceedings of the Royal Society of London B: Biological Sciences* 270: S147-S150.

IPCC. 2007. *Climate change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL, eds. New York, NY.

Jacobsen JB, Hanley N. 2009. Are there income effects on global willingness to pay for biodiversity conservation? *Environmental and Resource Economics* 43:137-160.

Kelly D, Kolstad C. 2000. Integrated assessment models for climate change control. *In* Folmer H, Tietenberg T, eds. *International Yearbook of Environmental and Resource Economics 1999/2000: A Survey of Current Issues*. Cheltenham, UK: Edward Elgar.

Kerr JT, Kharouba HM. 2007. Climate change and conservation biology. *In* May R, McLean A, eds. *Theoretical Ecology: Principles and Applications*. Oxford, UK: Oxford University Press.

Kinzig AP, Harte J. 2000. Implications of endemics-area relationships for estimates of species extinctions. *Ecology* 81:3305-3311.

Kramer RA, Sharma N, Nunasinghe M. 1995. Valuing Tropical Forests: Methodology and Case Study of Madagascar. World Bank Environment Paper 13.

Kramer RA, Mercer DE. 1997. Valuing a global environmental good: U.S. residents' willingness to pay to protect tropical rain forests. *Land Economics* 73(2):196-210.

Lewis OT. 2006. Climate change, species-area curves and the extinction crisis. *Philosophical Transactions: Biological Sciences* 361:163-171.

Loreau M. 2010. *From Populations to Ecosystems: Theoretical Foundations for a New Ecological Synthesis*. Princeton, NJ: Princeton University Press.

MacArthur RH. 1972. *Geographical Ecology: Patterns in the Distributions of Species*. New York, NY: Harper & Row.

Malcolm JR, Markham A, Neilson RP, Garaci M. 2002. Estimated migration rates under scenarios of global climate change. *Journal of Biogeography* 29:835-849.

Malcolm JR, Liu C, Neilson RP, Hansen L, Hannah L. 2006. Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology* 20(2):538-548.

Mastrandrea MD. 2009. Calculating the benefits of climate policy: examining the assumptions of integrated assessment models. Pew Center for Climate Change discussion paper. http://www.pewclimate.org/benefits-workshop/mastrandrea-calculating-benefits-of-climate-policy.

May RM, Lawton JH, Stork NE. 1995. Assessing extinction rates. *In* Lawton JH, May RM, eds. *Extinction Rates*, p 1-24. Oxford, UK: Oxford University Press.

McLachlan JS, Clark JS, Manos PS. 2005. Molecular indicators of tree migration capacity under rapid climate change. *Ecology* 86:2088-2098.

MEA (Millenium Ecosystem Assessment). 2005a. *Ecosystems and Human Well-being: Biodiversity Synthesis*. Washington, DC: Island Press.

MEA (Millenium Ecosystem Assessment). 2005b. *Ecosystems and Human Well-being. Volume 2: Scenarios*. Washington, DC: Island Press.

Menzel A, Estrella N. 2001. Plant phenological changes. *In* Walther GR, Burga CA, Edwards PJ, eds. *"Fingerprints" of Climate Change: Adapted Behavior and Shifting Species Ranges*, p 123-137. Plenum, NY: Kluwer Academic.

National Research Council. 1999. *Perspectives on Biodiversity: Valuing its Role in an Ever Changing World*. Washington, DC: National Academy Press.

National Research Council. 2005. *Valuing Ecosystem Services: toward Better Environmental Decision-Making*. Washington, DC: National Academies Press.

Newbold SC, Griffiths C, Moore C, Wolverton A, Kopits E. 2010. The "social cost of carbon" made simple. NCEE Working Paper # 10-07.

Nordhaus WD, Boyer J. 2000. *Warming the World: Economic Models of Global Warming*. Cambridge, MA: MIT Press.

Parmesan C. 2006. Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* 37:637-669.

Parmesan C, Ryrholm N, Stefanescu C, Hill JK, Thomas CD, Descimon H, Huntley B, Kaila L, Kullberg J, Tammaru T, Tennent WJ, Thomas JA, Warren M. 1999. Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399:579-583.

Parmesan C, Yohe G. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421:37-42.

Pearson RG. 2006. Climate change and the migration capacity of species. *Trends in Ecology and Evolution* 21:111-113.

Pearson RG, Dawson TP. 2003. Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology & Biogeography* 12:361.

Pereira HM, Leadley PW, Proenca V, Alkemade R, Scharlemann JPW, Fernandez-Manjarres JF, Araujo MB, Balvanera P, Biggs R, Cheung WWL, Chini L, Cooper HD, Gilman EL, Guenette S, Hurtt GC, Huntington HP, Mace GM, Oberdorff T, Revenga C, Rodrigues P, Scholes RJ, Sumaila UR, Walpole M. 2010. Scenarios for global biodiversity in the 21st century. *Science* 330:1496-1501.

Peterson AT, Tian H, Martinez-Meyer E, Soberon J, Sanchez-Cordero V, Huntley B. 2005. Modeling distributional shifts of individual species and biomes. *In* Lovejoy TE, Hannah L, eds. *Climate Change and Biodiversity*, p 211-228. New Haven, CT: Yale University Press.

Pimm SL, Russell GJ, Gittleman JL, Brooks TM. 1995. The future of biodiversity. *Science* 269:347-350.

Raudsepp-Hearne C, Peterson GD, Tengö M, Bennett EM, Holland T, Benessaiah K, MacDonald GK, Pfeifer L. 2010. Untangling the environmentalist's paradox: why is human well-being increasing as ecosystem services degrade? *BioScience* 60:576-589.

Richardson L, Loomis J. 2009. The total economic value of threatened, endangered and rare species: an updated meta-analysis. *Ecological Economics* 68:1535-1548.

Ritchie ME. 2010. *Scale, Heterogeneity, and the Structure and Diversity of Ecological Communities*. Princeton, NJ: Princeton University Press.

Roughgarden J. 2009. Is there a general theory of community ecology? *Biology and Philosophy* 24:521-529.

Root TL, Hughes L. 2005. Present and future phenological changes in wild plants and animals. *In* Lovejoy TE, Hannah L, eds. *Climate change and biodiversity*, p 61-74. New Haven, CT: Yale University Press.

Root TL, Price JT, Hall KR, Schneider SH, Rosenzweig C, Pounds JA. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421:57-60.

Sala OE, Chapin III FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M, Wall DH. 2000. Global Biodiversity Scenarios for the Year 2100. *Science* 287:1770-1774.

Smith JB, Schneider SH, Oppenheimer M, Yohe GW, Hare W, Mastrandrea MD, Patwardhan A, Burton I, Corfee-Morlot J, Magadza CHD, Fussel H-M, Pittock Ab, Rahman A, Suarez A, van Ypersele J-P. 2009. Assessing dangerous climate change through an update of the Intergovernmental Panel on Climate Change (IPCC) “reasons for concern.” *Proceedings of the National Academy of Sciences*

Svenning JC, Skov F. 2004. Limited filling of the potential range in European tree species. *Ecology Letters* 7:565-573.

Thomas CD. 2000. Dispersal and extinction in fragmented landscapes. *Proceedings of the Royal Society B: Biological Sciences* 267:139-145.

Thomas CD. 2005. Recent evolutionary effects of climate change. *In* Lovejoy TE, Hannah L, eds. *Climate Change and Biodiversity*, p 75-88. New Haven, CT: Yale University Press.

Thomas CD, Bodsworth EJ, Wilson RJ, Simmons AD, Davies ZG, Musche M, and Conradt L. 2001. Ecological and evolutionary processes at expanding range margins. *Nature* 411:577-581.

Thomas CD, Cameron A, Green RE, Bakkenes M, Beaumont MJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL, Williams SE. 2004a. Extinction risk from climate change. *Nature* 427:145-148.

Thomas CD, Williams SE, Cameron A, Green RE, Bakkenes M, Beaumont MJ, Collingham YC, Erasmus BFN, de Siqueira MF, Grainger, Hannah L, Hughes L, Huntley B, van Jaarsveld AS, Midgley GF, Miles L, Ortega-Huerta MA, Peterson AT, Phillips OL. 2004b. Biodiversity conservation: Uncertainty in predictions of extinction risk/Effects of changes in climate and land use/Climate change and extinction risk (reply). *Nature* 430. DOI: 10.1038/*nature*02719.

Thomas CD, Franco AMA, Hill JK. 2006. Range retractions and extinction in the face of climate warming. *Trends in Ecology and Evolution* 21:415-416.

Thuiller W, Araujo MB, Pearson RG, Whittaker RJ, Brotons L, Lavorel S. 2004. Biodiversity conservation: uncertainty in predictions of extinction risk. *Nature* 430. DOI: 10.1038/*nature*02716.

Tol RSJ. 2002a. Estimates of the damage costs of climate change. Part 1: benchmark estimates. *Environmental and Resource Economics* 21:47-73.

Tol RSJ. 2002b. Estimates of the damage costs of climate change. Part 2: dynamic estimates. *Environmental and Resource Economics* 21:135-160.

Travis JMJ. 2003. Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society of London B: Biological Sciences* 270:467-473.

Ulrich W. 2005. Predicting species numbers using species-area and endemics-area relations. *Biodiversity and Conservation* 14:3351-3362.

Walther GR. 2000. Climatic forcing on the dispersal of exotic species. *Phytocoenlogia* 30:409.

Walther GR, Beissner S, Burga CA. 2005. Trends in the upward shift of alpine plants. *Journal of Vegetation Science* 16:541-548.

Walther GR, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. *Nature* 416:389-395.

Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. *Nature* 414:65-69.

Willis KJ, Bhagwat SA. 2009. Biodiversity and climate change. *Science* 326:806-807.

Tables and Figures

Table 1. Temperature change scenarios, estimated biodiversity losses, and the associated calibrated biodiversity loss parameters, based on two recent studies of the effects of climate change on species extinctions. For each scenario, ΔT [^{o}C] is the constant annual temperature change, H [yr] is the time horizon, and L_H is the prediction fraction of species committed to extinction by the end of the time horizon.

	ΔT	H	L_H	Implied φ
Thomas *et al*. 2004	0.025	50	0.18	6.33
	0.038	50	0.24	3.79
	0.060	50	0.35	2.38
Malcolm *et al*. 2006	0.050	100	0.01	0.040
	0.050	100	0.116	0.49
	0.050	100	0.43	2.24
			Best fitting estimate =	1.21

Table 2. Calibrated value function parameters based on two economic valuation studies, Kramer and Mercer (1997) and Richardson and Loomis (2009).

Source study	Avg. *WTP*	Species ranks	β	λ	$WTP(+5\%)$	$WTP(+50\%)$
Kramer & Mercer 1997	$48	NA	2.30×10^{-8}	NA	$270	$2,100
	$33	NA	1.58×10^{-8}	NA	$190	$1,500
Richardson & Loomis 2009	$380 , $22	200 , 20	3.75×10^{-7}	0.016	$1,600	$9,400
	$380 , $22	100 , 10	1.87×10^{-7}	0.032	$800	$5,600
	$380 , $22	50 , 5	9.05×10^{-8}	0.063	$390	$3,000
	$380 , $22	20 , 2	3.54×10^{-8}	0.156	$160	$1,200
	$380 , $22	10 , 1	1.68×10^{-8}	0.305	$74	$600
		Best fitting estimates =	9.50×10^{-8}	0.015		

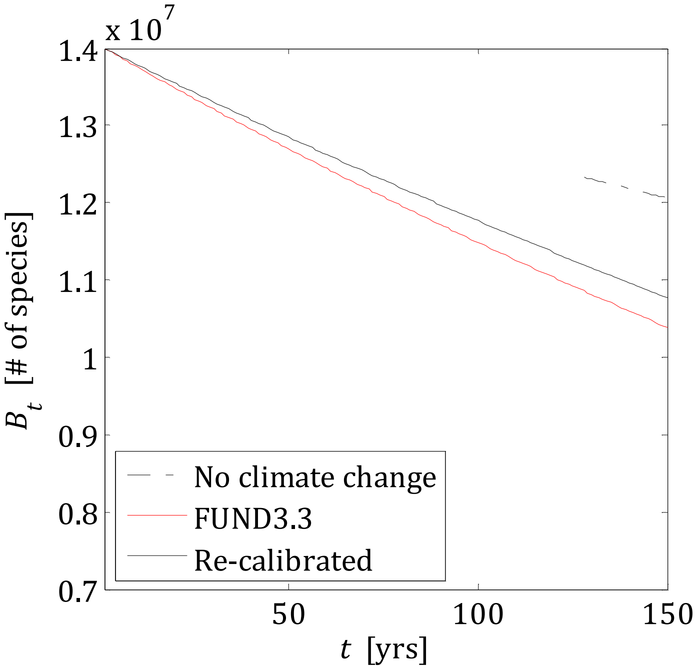

Figure 1. Projections of global biodiversity loss under no climate change, and with climate change using the central parameters in FUND3.3 and using the re-calibrated parameters based on the results of Thomas *et al*. (2004a) and Malcolm *et al*. (2006).

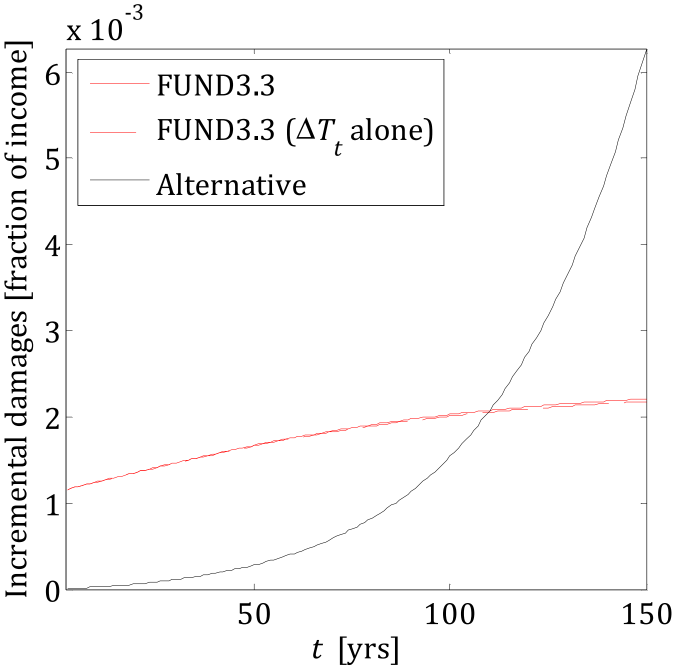

Figure 2. Projections of incremental ecosystem damages using FUND3.3 and the willingness to pay to avoid global biodiversity loss using our alternative value function as a fraction of income for a representative agent with starting income of $30,000 per year, growing at 2 percent per year, under a scenario with temperature increasing by 0.025 deg C per year.

Appendix 1. List of variables referred to or utilized in this manuscript.

Variable	Definition (parameter values of constants)	Appears in equation(s)
ΔT_t	temperature change between year *t-1* and *t*	1
φ	sensitivity of global biodiversity to extinction via global temperature change	1, 2, 3
θ	background rate of biodiversity loss, independent of climate change	1, 2, 3
B_t	global species richness at year *t*	1, 4, 6, 7, 8, 10
B_H	estimated level of global biodiversity in some future year, *H*, if temperature is constant	2
B'_H	estimated level of global biodiversity in some future year, *H*, under a constant annual temperature change scenario	2
H	time horizon (number of years in the future from reference year)	2, 3
L_H	fraction of species “committed to extinction” or “threatened by extinction” at some future year, *H*	2, 3
ΔT	annual change in temperature	2, 3
B_0	Global biodiversity (species richness) estimated for the year 2000	2, 4, 5
d_{tr}	per capita economic damage in year *t*, for a representative resident of region *r*	4
ΔT_{tr}	temperature change between year *t-1* and *t* in region *r*	4
y_{tr}	average per capita income in year *t* and region *r*	4
α, ω, ψ, τ, σ	FUND ecosystem damage function parameters	4
p_{tk}	probability that species *k* is not extinct at time *t*	5
V	present value of utility for a representative individual	5
t	annual period	5, 6, 7, 8
ρ	pure rate of time preference, or utility discount rate	5, 8, 9
β	preference parameter reflecting the marginal utility of the biodiversity index	5, 8, 9, 10
η	constant relative rate of diminishing marginal utility of consumption	5, 8, 9, 10
k	index of species value ranks by a representative individual	5, 9
λ	preference parameter reflecting rate at which value weights decline with species rank	5, 9
y_t	individual’s income at time *t*	5, 10
A_0	current area of non-rainforest habitats	6
c_A	species-area coefficient for non-rainforest habitats	6
c_R	species-area coefficient for rainforest habitat	6

R_0	current area of rainforest habitat	6
P	currently protected fraction of rainforests	6, 7
Q	additional fraction protected under the hypothetical scenario of the stated preference survey	6, 7
z	fitted exponent in species-area relationship	6, 7
δ	rate of habitat loss	6, 7
ΔB_t	change in global species richness between year *t-1* and year *t*	6, 7, 8, 10
WTP	lump sum willingness to pay	8
WTP_k	lump sum willingness to pay to protect species of rank *k*	9
wtp_t	willingness to pay in year *t*	10
A	area	-
$\hat{B}_t$	rate of biodiversity loss over time	-
c	leading coefficient in species-area relationship	-
L	fraction of species lost as a result of habitat loss	-
S	number of species	-
$\hat{y}_t$	growth rate of income over time	-