

ECOLOGICAL CONSEQUENCES OF DOUBLING THE ATMOSPHERIC CO₂ CONCENTRATION

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Abstract. Increasing atmospheric concentrations of CO₂ have been linked to corresponding increases in surface temperatures. The CO₂ concentration is expected to reach double the pre-industrial level during the next century. In this synthesis paper, I attempt to trace *the global and local responses to a hypothetical instantaneous doubling of the atmospheric CO₂ concentration*. In this worst-case scenario, the *global system* would respond in complex ways to the CO₂ perturbation over short and long time scales. I use a simplified process model to conceptually sequence and trace the temporal responses of various domains within the global system, including some critical feedbacks between different domains. I also introduce the concept of *asynchronous range shifting* of species as a major response to warmer climates, and describe how this could trigger a major reshaping and restructuring of natural communities over long time periods. I conclude with a case study of a migratory bird community illustrating some of the ecological responses discussed in this paper.

INTRODUCTION

Increases in the atmospheric concentrations of greenhouse gases such as carbon dioxide (CO₂), methane and water vapor have been directly linked to increases in the global mean surface temperatures. Recent studies have shown a historical correlation between the concentrations of greenhouse gases and the Antarctic air temperatures over the last 420,000 years (Petit 1999). Since the beginning of the industrial revolution, the CO₂ concentration has increased from about 275 ppm to the current level of about 360 ppm (Gates 1993), primarily due to the burning of fossil fuels and to a lesser extent due to other human activities such as deforestation. The mean annual global surface temperature has increased by about 0.6 °C in the last 130 years.

At the current rate of fossil fuel usage and deforestation, it has been estimated that the CO₂ concentration could reach about 600 ppm during the next century, which represents a doubling of the pre-industrial level. This is expected to result in average temperature increases of 1-3.5 °C as compared to 1990 (UNEP and WMO 1992), as well as an increase in the difference between summer and winter temperatures. The combination of higher CO₂ levels and increased temperatures could lead to major ecological consequences around the world.

In this paper, I have attempted to trace the *short-term and long-term ecological consequences of a hypothetical instantaneous doubling of the CO₂ concentration* relative to the pre-industrial level (the “2xCO₂” scenario), rather than a gradual increase over many decades. This is an interesting worst-case scenario, which simply uses the current estimate of CO₂ increase over the next century, but allows no time for any human intervention to reduce the CO₂ emissions. The global system, defined here as consisting of all the biotic and the abiotic components, would react to this CO₂ perturbation, over various time scales, through its biogeochemical cycles, local ecosystems and the organisms that live in the ecosystems.

I have developed a diagrammatic process model to illustrate the responses and interactions over time of the various natural systems that would be affected by a 2xCO₂ regime. The temporal scale for the ecological predictions ranges from the immediate short-term (a few months to a few years) to the very long-term (up to a few centuries). The spatial scale for the predictions is both global and local. I first describe the predicted responses of the global system, and then use a case study to illustrate some of the specific ecological responses and consequences as seen from a local ecosystem. The predictions themselves are of a qualitative nature, due to substantial uncertainties and our incomplete knowledge in this entire area.

OVERALL RESPONSES OF THE GLOBAL SYSTEM

Fig. 1 presents a process model that will be used in the remainder of this paper. For clarity of presentation, I have partitioned the entire global system into three domains. *The atmospheric system* basically transforms the concentrations of the greenhouse gases into annual

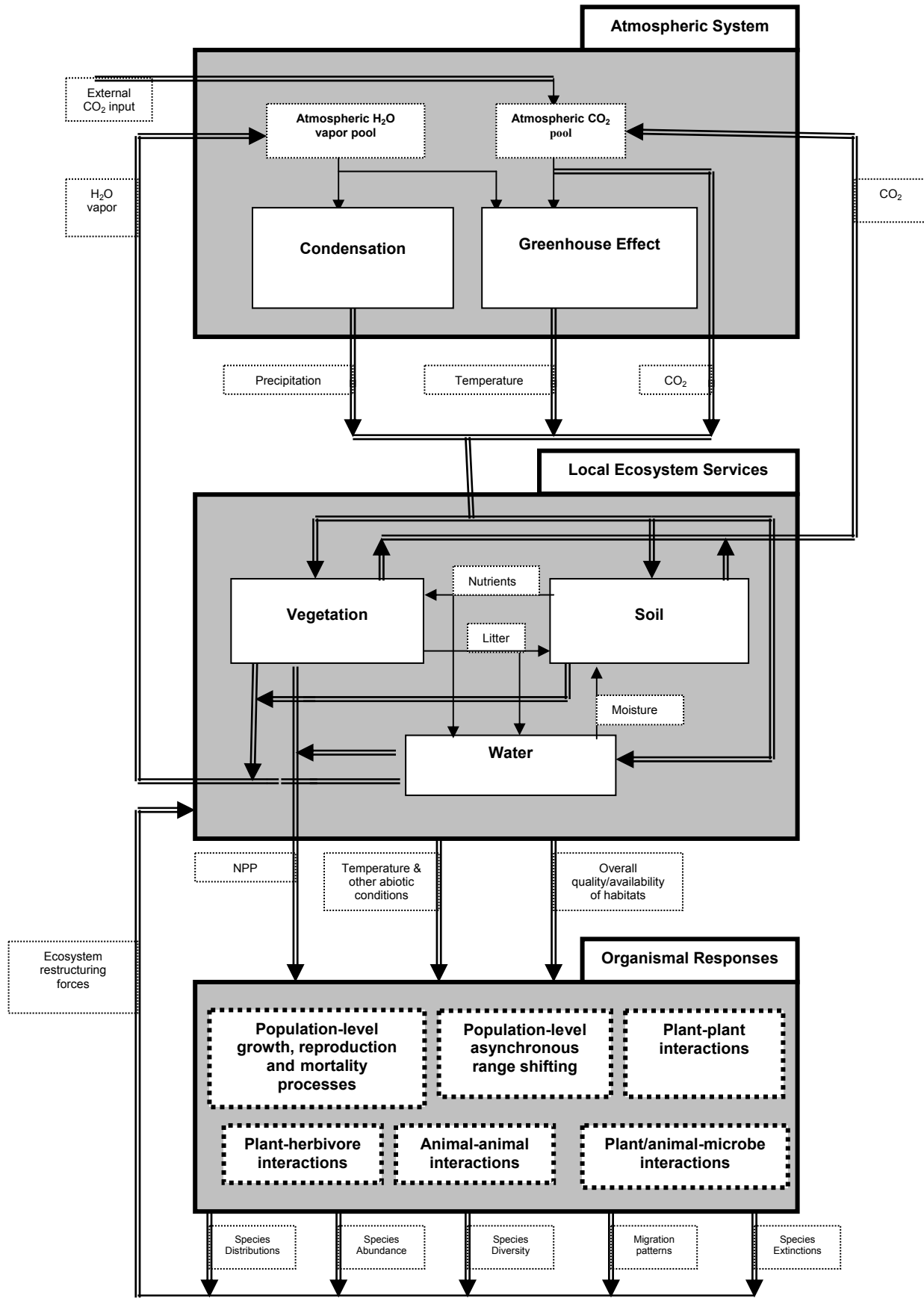


FIG. 1. The Process Model

temperatures (mean, minimum and maximum) at various latitudes and elevations around the earth. It also converts water vapor into precipitation. The *local ecosystem services* consist of the basic vegetation, soil and water that provide services (such as habitats, conversion of solar energy into food, and other conditions/resources necessary to sustain life) to the hierarchy of organisms that are part of an ecosystem. The *organismal response system* includes the biology and the behavior of all the plants, animals and microbes that live within various ecosystems.

Immediate short-term: Atmospheric Responses

The earth's atmosphere absorbs solar radiation and maintains a global energy balance by re-radiating some of the energy back into space in the form of infrared radiation (Raval 1989). This escaping energy is smaller than that emitted by the earth's surface, and the difference is trapped in the atmosphere by greenhouse gases that absorb infrared radiation in the 8-14 μm wavelengths. For the 2xCO₂ scenario, the result is an increase in the average surface temperatures around the globe by about 1-3.5 °C, and the increases are expected to be higher at latitudes above 50-70° by a factor of 2 compared to latitudes closer to the equator. At these higher latitudes, winter temperatures are expected to increase more than summer temperatures, resulting in a widening range of temperatures over an annual period. At higher temperatures, the annual precipitation can also be expected to increase by about 7-11% (Fields 1993), due to additional evaporation and transpiration.

These direct temperature effects of 2xCO₂ can be expected in the immediate short-term, such as *a few months to a few years* from the time of the CO₂ perturbation. The outputs of the atmospheric system, as illustrated in Fig. 1, consist of three categories of measurable variables that capture the immediate short-term effects: global atmospheric CO₂ concentration; mean and extreme annual surface temperatures around the globe; and the average annual precipitation around the globe. The temperature predictions also include the effects some of the feedbacks to be discussed in the next section.

Short/medium-term: Initial Ecosystem Responses

In Fig. 1, the local ecosystem services domain includes the following: the terrestrial vegetation, including its pools of carbon, nitrogen and other nutrients; the soil, including its pools

of carbon, nitrogen and other nutrients; and all the water, including ponds, lakes, rivers and oceans. *On a time scale that covers the short-term and the medium-term (i.e., up to 10 years)*, there should be measurable changes in the outputs of the local ecosystem services domain.

The net primary productivity (NPP), from both terrestrial and aquatic producers, is one of the critical outputs of the ecosystem services domain. Higher CO₂ levels would generally result in increased photosynthesis, reduced photorespiration, lower stomatal conductance, and more vegetative reproduction (i.e., more branching, rooting and tiller production), with the responses dependent on the levels of other nutrients, water and light (Strain 1987; Bazzaz 1990). Warmer temperatures also increase the growth rate of most plants, particularly near the center of their climate ranges (Gates 1993). The carbon/nitrogen (C/N) ratio is expected to be higher, which would affect the feeding efficiency of herbivores including insects. Computer simulations predict that the short-term primary production of tropical and dry temperate ecosystems will be dominated by CO₂ levels, while northern and moist temperate ecosystems will be limited by how much the nitrogen availability is enhanced by the higher temperatures (Melillo 1993).

The increased temperature due to 2xCO₂ would trigger additional evaporation and transpiration, which in turn would increase the water vapor content of the atmosphere. Water vapor is a potent greenhouse gas capable of amplifying the original CO₂ perturbation by a factor of 2 through *positive feedback* (Raval 1989). The temperature increase would also cause additional plant and soil respiration, adding to the CO₂ concentration further. Thus, CO₂ and water vapor are additional outputs of the ecosystem services domain that feed back into the atmospheric system, as mentioned previously. (Methane is not considered in this paper.)

There would also be changes in the quality and availability of other resources and conditions and generally changes to the overall habitats of various organisms that live within an ecosystem. These ecosystem “outputs” are particularly difficult to quantify and generalize, and the available data is quite sparse. In the following paragraphs, I briefly review a representative sample of the published forecasts that relate to specific ecosystem types, in order to illustrate the complexity and the range of issues that must be considered at the ecosystem level (Bazzaz 1990; Poiani and Johnson 1991; Meyer and Pulliam 1992).

Tundra ecosystems: The higher temperatures would extend the growing season, expose more peat to the more active decomposers, and lower the water table through higher transpiration. Decreased insulation and the resultant lowering of the permafrost table, as well as increased soil erosion, would offset the increase in nutrient availability. Under 2xCO₂, the wet tundra ecosystems could change from a net CO₂ sink into a net CO₂ source.

Estuarine marshes: In sharp contrast with the tundra ecosystems, the C/N ratio is not likely to be affected in estuarine marshes due to continued input of nutrients in the water flowing from adjacent creeks. High CO₂ levels may cause continued increase in primary productivity.

Grasslands: High CO₂ levels will enhance growth in C3 plants, but this is not expected in C4 plants. Further, the short growing season and limited nutrient availability could dampen the effects of elevated CO₂ levels for these low-stature communities.

Coastal wetlands: Rising sea levels from melting icecaps and thermal expansion could flood salt-grass marshes, and generally reduce the size and productivity of the intertidal zone.

Prairie wetlands: The North American Great Plains could become significantly warmer under 2xCO₂ (mean summer temperatures up by 1-2 °C; mean winter temperatures up by 3-4 °C). One of the consequences would be lower water levels in the semipermanent wetlands, which would normally have water throughout the growing season. As a result, some wetlands would become completely closed with vegetation, while the salinity would increase in others. The annual waterfowl production could be directly reduced due to this reduction in habitat quality and availability.

General terrestrial-aquatic ecosystem interactions: The decreased stomatal conductance in a 2xCO₂ regime would decrease the water consumption of plants and increase the proportion of the precipitation that results in runoff. The leaf litter entering streams would have lower nitrogen content, with ramifications for litter decomposition rates in streams. Also, if the food quality of the terrestrial herbivores is reduced due to higher C/N ratios, then they may compensate by eating more and consequently less leaf litter would enter the streams. In addition, under higher temperatures, the respiration of soil organic matter would be accelerated, resulting in a decrease in the amounts of dissolved organic carbon leached from soils and transported to streams.

Medium/long-term: Organismal Responses

In Fig. 1, the organismal response system includes much of the biology and the behavior of the organisms that are part of various ecosystems, in the context of their responses to such factors as 2xCO₂, elevated temperature, modified habitats, and changes to food sources. While plants were included as short-term primary producers in the context of ecosystem services, they are included again within this domain as organisms in their own right. The organismal response includes all the interactions within each species and between different species. It includes the individualistic response of organisms as well as the collective response of entire species. These responses may be expected *on a time scale covering the medium-term to the long-term (i.e., from a few years to several decades, or up to several centuries in some cases)*.

The effects of a 2xCO₂ regime on the intraspecific and interspecific interactions of organisms are likely to be very complex and are not well understood at this point. In an experiment with annual plants (Bazzaz 1990), elevated CO₂ levels magnified the intensity of plant-plant interactions and enhanced the growth of only the dominant individuals. The competitive success of some species (as measured by such factors as biomass and reproductive allocation) could be directly influenced by CO₂ levels. For example, it is known that C3 plants can out-compete C4 plants in a CO₂-rich environment, since photorespiration in C3 plants would be reduced by the higher atmospheric CO₂ levels.

Tissue quality of plants, as measured by the C/N ratio, would be altered in a 2xCO₂ environment, and this would affect the fitness of insect herbivores. They would have to increase their consumption rates by 20-80%, and/or suffer from slower growth (Bazzaz 1990). They would be more vulnerable in general to predators and parasitoids, with a reduced likelihood of completing their development in seasonal environments.

One of the better-understood aspects of climate change at the organismal level is the change in species' geographical ranges and composition on regional spatial scales. Most plant and animal species have optimal temperature ranges within which they experience peak performance. As the global climate becomes warmer, many species may not be able to acclimate to the new

conditions and are likely to shift their geographical ranges towards the poles or to higher elevations where the temperatures might be more suitable.

Insects are highly sensitive to temperature changes and studies based on natural populations of butterflies (Parmesan 1996; Parmesan et al. 1999) have been very revealing. There has been a clear poleward shift in the ranges of many non-migratory European butterfly species by 35-240 km during this century and these shifts have been closely correlated with temperature increases. These changes to distributions occur at the population level, due to changes in the ratios of extinctions to colonizations at the northern and southern boundaries of the range. Since most wildlife is sedentary, such changes would occur slowly and would be measurable as a range shift towards the poles.

Northward range shifts of invertebrate fauna of California's rocky intertidal community has been observed over the 60-year period from the early 30's to the early 90's (Barry et al. 1995), again tracking a period of climate warming. Increasing species richness of Alpine flora has been observed at higher elevations and mountain summits, indicating an elevational change in their ranges likely due to warmer temperatures (Grabherr et al. 1994).

For species that are not sedentary, such as birds, large-scale studies have been performed (Root 1988a; Root 1988b) which show that physiological demands restrict the northern boundaries of wintering birds. One of the limiting factors appears to be the maximum metabolic rate, which tends to be around 2.45 times the basal metabolic rate for the bird species in these studies. This, in turn, limits how far north these birds can move and still sustain themselves by feeding and maintaining body temperature through higher metabolic rates. It would seem that these birds could shift their northern boundaries further if the winter temperatures were to increase by a few degrees in a 2xCO₂ regime.

The geographical ranges of many species appear to be correlated with the minimum and maximum annual temperatures of those regions, which could be used to predict new ranges for the species based on a new temperature profile of the earth (Jeffree and Jeffree 1996). Even though other factors besides temperature must necessarily be included in such predictions (Davis

et al. 1998), there seems to be a reasonable amount of evidence that temperature is one of the main limiting factors to the distribution of species.

Each species is likely to react in a unique way to higher CO₂ levels and temperatures. As species shift their ranges towards the poles in response to a warmer climate, different species will move at different speeds. Plants will move the slowest over very long time periods, possibly over several centuries in some cases, through colonization (via seed dispersal) and extinctions. Sedentary animals will move the next slowest, perhaps over time periods of many decades, and will be constrained by the availability of suitable new habitats at higher latitudes. The more mobile species, such as migratory birds and fishes, will be able to move the fastest. In addition to the direct effect of warmer temperatures, there would be indirect effects such as changes in the quality and availability of habitats. These indirect effects could act as additional factors determining the direction and magnitude of range shifts. It seems quite certain that different species from a particular community will move at different speeds and to different geographic areas. This would lead to the phenomenon of *asynchronous range shifting* at the community level and result in completely new communities being formed in unpredictable ways.

Plant species would be particularly vulnerable for two reasons. First, their migration and regeneration rates would be much slower than the climate change itself, possibly resulting in the deaths of many individual plants and a general reduction in plant diversity (Bazzaz 1990; Poiani and Johnson 1991). Second, plants have a strong mutualistic relationship with animals – plants provide food, and receive services such as seed dispersal and pollination. Due to asynchronous range shifts of different species, it might be difficult to maintain this delicate balance.

Animal species would also be at risk due to uncertainties in food supplies and suitable habitats in their new ranges. In the long-term, any reduction in plant diversity and abundance could further affect the diversity and abundance of animal species. It is also possible that entirely new competitive interactions could develop in the newly forming communities. Thus, the range shift phenomenon may well become one of the strongest driving forces for ecosystem restructuring.

Very long-term: Ecosystem Restructuring Responses

The outputs of the organismal response system include such variables as the distribution and abundance of species on local spatial scales, the mix (diversity) of species on local scales, global migration patterns, and extinctions of species. Interestingly, these are much more measurable than the outputs of the local ecosystem services domain, *although the measurements in some cases may have to span multiple centuries*. Together, these outputs constitute the *ecosystem restructuring forces* in Fig. 1. These outputs are part of a major feedback path, based on the responses of populations and communities, which could dramatically change entire ecosystems. The modified ecosystems, in turn, could further influence the climate through other feedback paths. It seems likely that many ecosystems would be in a state of disequilibrium due to the feedback paths, and regenerating ecosystems may well dominate much of the landscape for many centuries.

A CASE STUDY: MIGRATORY BIRDS

In this section, I consider a case study of how a migratory bird community might potentially be affected by the temperature increases in the 2xCO₂ regime. While the temporal scale ranges from the short-term to the long-term as before, the spatial scale is restricted to the main nesting habitats and migratory routes of the bird community. The ecosystem and organismal responses can then be seen strictly from the point of view of this community.

Arctic-breeding shorebirds, such as the Arctic tern, nest on the flat, open tundra among mosses, lichens and low-growing plants (Gates 1993). During their northward migration in the spring, many of these birds stop along Delaware Bay to feed on the eggs of horseshoe crabs. Their major food source during the nesting period consists of insect hatches that start occurring around the time of their arrival.

For the insect species in the tundra, the only reasonable short-term biological response to higher temperatures would be to reproduce earlier in the year, perhaps by several weeks, in synchrony with their ideal spawning temperature. If these insect hatches occur before the birds arrive in the spring, then the birds would not be able to obtain enough food and gain enough

weight before their southern migration in the autumn. In addition, the horseshoe crabs would exhibit a similar short-term response by spawning earlier, leaving the birds with insufficient food on their northern migratory route. From the point of view of the birds, *these responses of their food sources could be seen as part of the initial ecosystem responses*, even though my original definition of the local ecosystems services domain did not include as outputs any food sources other than NPP. The bird population would experience some decline in the short-term as a result of these initial ecosystem responses.

Over a longer period (a few years to a few decades), additional responses would be dominated by the cascade of organismal responses. The vegetation in the tundra could change due the northward range shifts of plant species. If taller-growing shrubs move in, the nesting habitats of these birds would be severely disrupted. During this same period, their main food source might decline further. At this high latitude, the insect species would not be able to shift their ranges any further to compensate for the temperature increase, resulting in higher mortality rates and lower fecundity. The native insect species might eventually become extinct in this region. In addition, the change in the vegetation structure might accommodate other insect species that may be gradually shifting north from more southern latitudes. Even if some of these new insect species were suitable sources of food, the birds would still have to adapt to nesting in a different habitat. As with insects, range shift would not be an option for bird species that are already at high northern latitudes.

On the other hand, other migrating bird species might now be able to reach further north during the spring and summer; i.e., both their northern and southern boundaries could shift northward depending on the summer and winter temperature extremes (see earlier discussion on the northern boundaries of wintering birds). Other non-migratory species, including new predators, might also undergo northward range shifts and reach the tundra. The survival of the arctic-breeding shorebirds in the tundra would depend on a combination of several factors: adaptation to different food sources; adaptation to new nesting habitats; ability to find a competitive niche in the presence of potential rivals among the other migrating bird species; and, ability to find sufficient “predator-free” space.

In addition, the migratory patterns of these arctic-breeding birds could be impacted. The increase in the winter temperature at their southern destinations could cause them to find alternative wintering sites, most likely at higher latitudes. The availability of intermediate resting points and food sources along the migratory paths could modify both the paths and the destinations.

The interaction of the arctic-breeding shorebirds with other species, as all the species exhibit differing responses to the climate change, would contribute to the *ecosystem restructuring forces*. One of the underlying driving forces is clearly the range shift phenomenon, as well as the reduced ability of species at high latitudes to shift their ranges further. Overall, this qualitative analysis indicates the possibility of a significant decline in the population of these birds in the best case, and perhaps a complete extinction in the worst case, over a period of several decades. This example also demonstrates the use of the simplified process model as a tool for structuring and understanding the sequence of temporal responses of a particular ecological community to a warmer climate.

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