vide no information on regional variations.

To advance sea-level projections, particularly at the regional level, it is crucial to understand the dynamical interactions between the ice sheets and the oceans, quantify changes in precipitation over Antarctica, advance understanding of the ocean's dynamic response to climate change, and continually monitor the ongoing changes. Given the difficulties and time required to develop fully coupled Earth system models that include full-stress ice-sheet models (11) that can reliably project sea-level rise, it is important to question and understand the accuracy and fidelity of the semi-empirical models. Resolving the discrepancies between these two approaches

may lead to new projections that exploit advantages of both and may provide more reliable scenarios in a timely fashion.

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### Supplementary Materials

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CLIMATE CHANGE

## **Modeling Ice-Sheet Flow**

Richard B. Alley1 and Ian Joughin2

The great Greenland and Antarctic ice sheets are the "wild cards" in projections of sea-level change (1). Early models of the coupled ocean-atmosphere system treated the ice sheets as static white mountains. Observations since then have shown that ice sheets can change quickly (2): In some places, the tides strongly modulate coastal ice flow; in others, warming-induced iceshelf loss has caused the flow

speed of the subsequently unbuttressed inland ice to increase almost 10-fold within a few weeks (3, 4). A new generation of full-stress ice-sheet models incorporates the physics needed to reproduce such processes (see the figure) (5–7). Including full stresses does improve ice-flow simulations (8). Well-validated, robust projections of ice-sheet behavior under climate change nevertheless remain a challenge, as they will require an ensemble of model ice sheets coupled to the rest of the climate system.

Part of the computational difficulty in ice-sheet modeling arises from the ordersof-magnitude variations of the frictional drag at the ice bed and margins that balances the gravitational driving stress. Although the gov-

erning equations have long been known, they are numerically challenging to solve. Earlier models relied on simplified representations of how ice flow redistributes these stresses from low-drag to high-drag regions. In contrast, the new models include all stresses without simplifying assumptions, and offer improved coupling to the ocean and atmosphere, in an era when computing speeds are beginning to make such approaches feasible.

Despite advances in the speed, stability, comprehensiveness, and coupling of models, difficulties remain. Even full-stress models are limited by poor knowledge of the bedrock surface on which the ice rests, where features a few kilometers or less in extent may be important to ice flow. The location of these features in Earth's more remote areas and beneath kilometers-thick, continental-scale sheets of ice makes them difficult to measure at the necessary scale. Programs such as NASA's Operation IceBridge are beginning to collect data Full-stress flow models for ice sheets promise improved projections of sea-level change.

Complex crevasses on Pine Island Glacier, West Antarctica. A new generation of ice-flow models allows simulation of the stress states that give rise to crevasse patterns and their effect on the ice (15).

at the scale necessary to address this problem.

Also, understanding of where freezing fixes the ice to its bed and to what extent melting facilitates fast basal motion remains limited. The bed's thermal state is in part determined by the geothermal flux, which has yet to be measured anywhere beneath an ice sheet with sufficient accuracy and extent to usefully constrain the frozen-thawed boundary. In addition, ice deformation increases exponentially with temperature and is influenced by flow-induced preferred orientations of the anisotropic ice crystals; yet, few direct icecore and borehole measurements of anisotropy and temperatures exist for the deep ice layers that control deformation. Geophysical techniques can be used to interpolate these data between core sites and to map the frozenthawed boundary and the distribution of lubricating till, but insufficient data exist to allow detailed estimates for entire ice sheets.

Until sufficient data are produced (if ever), ice-sheet models must rely on assimilation of surface velocities and other available data to estimate the unknown quantities. A difficulty is that differently parameterized models applied to regions where the ice flow is currently not changing may provide statistically similar fits to modern data but very different responses to future forcing. Such ambiguities about future response can, however, often be

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resolved in places where large recent changes have occurred (9), providing a basis for process understanding that can be extrapolated to regions that are still stable.

Guidance for integrating the new glaciological models with existing research can be gained from the experience of the Intergovernmental Panel on Climate Change and related efforts to assess likely ocean-atmosphere change. The results presented to policy-makers with greatest confidence are those that are derived from fundamental physics, are seen in a hierarchy of models for physically similar reasons, and have been successfully "retrodicted" in paleoclimatic and instrumental records; failure of any of these reduces confidence.

A coordinated modeling effort is essential to gain the understanding and achieve the successful retrodiction that increase confidence in projections. However, a measure of heterogeneity in such activity is just as important. The mean behavior of ~20 general circulation models matches observed climate data much better than any single model (10), providing reason to doubt the apparent efficiency of moving forward with one model.

The improvement provided by full-stress models comes at a large computational cost, leaving much room for nimble but simplified models. For example, the need to test against paleoclimatic archives, together with the >100,000-year time scales of central ice-sheet regions, cannot be met with the full-resolution versions of the most complex models. Also, performance of simpler models is easier to test in situations with analytic solutions. During assimilation and forward

modeling, uncertainties in a host of parameters can affect outcomes; "massive ensemble" analyses (11), which show whether particular solutions are excluded, allowed, or likely, are almost entirely the realm of simplified models. Comprehensive model runs can be viewed as numerical experiments; efforts to understand the outcomes of such experiments at a more fundamental level can provide important insights to the climate system (12, 13). Thus, the advent of the comprehensive modeling tools is likely to increase the need for simpler models.

Complex modeling is far from the only challenge on the road to useful ice-sheet projections. Model results and data both show that ice sheets can exhibit threshold behavior (14), which may depend on small features that are not well sampled by available data sets. Maintenance of observational capacity, from ice cores to satellites, will be crucial to ensure that current and future ice-flow and ice-thickness changes are measured. The lack of a firm understanding of ice-sheet—ocean interaction, constrained by reliable ocean data, remains a critical obstacle to understanding future changes.

Still, there is cause for optimism. With the ability to determine thickness, speed, elevation change, and other characteristics of the ice sheets from space and aircraft, to survey them from the surface, to plumb their depths with cores, and to model them with a hierarchy of approaches, including full-stress models coupled to global climate models, today looks like the start of a new phase of glaciological research. Until rigorous model-based sea-level projections can be brought to frui-

tion, however, guidance is likely to continue to rely on semi-empirical approaches (1), analogy to paleoclimatic situations, physically limiting estimates, expert elicitations, and results of simpler models.

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**ECOLOGY** 

# **Impacts of Biodiversity Loss**

**Bradley Cardinale** 

ary biologists have treated the variety of life on Earth as if it were a simple by-product of the physical and chemical variation that generates biological diversity and allows it to persist. However, this perspective changed in the 1990s, when scientists began to manipulate biodiversity in controlled environments and found that it can act as an independent variable that directly controls

ecosystem-level functions, such as nutrient cycling and biomass production (1-4). The idea that biodiversity might control—rather than just respond to—Earth's biophysical processes was foreign to many researchers (5). But by 2010, more than 600 manipulative experiments had been performed, spanning much of the tree of life and most major biomes on the planet (6). We now know that biodiversity regulates many ecosystem-level processes, including some that are essential for providing goods and services to humanity (6-9). On page 589 of this issue, Reich et al. (10) provide important novel insights into

How much diversity is needed to maintain the productivity of ecosystems?

how much diversity is needed to maintain the productivity of ecosystems.

The authors reanalyze data from two classic biodiversity studies that have been running for more than a decade at the Cedar Creek Ecosystem Science Reserve in Minnesota. By fitting data collected over a 15-year period to several mathematical functions (linear, log, power, and hyperbolic), the authors quantify the form of the relationship that describes how plant species richness influences the production of plant biomass. They show that the effects of biodiversity on productivity change from saturating functions that are prominent

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