Figure 2 | Rifting in the Afar in 2005 in simplified cross-section. Movement on the fractures was mostly limited to the uppermost 2 kilometres of the crust, modelled by Wright *et al.*[1] as slip of up to 7 metres on two inclined fault planes. Farther below, magma did the splitting, forming a dyke that displaced adjacent plates by 2–4 metres in each direction. No source of co-rifting deformation is detected in a possible ductile region below about 9 km; total crustal thickness is about 20 km. The dyke was supplied by magma chambers below the Gabho and Dabbahu volcanoes, and possibly by a deeper source.

Gulf of Aden ridge meets the Afar rift. A smaller-scale rifting episode occurred in Djibouti in 1978 (refs 9, 10). The 1975–84 Krafla episode in Iceland[4,7,11], however, was more similar to the events of 2005 in Ethiopia in terms of its cumulative widening, the magma volume involved, and the importance of subsurface dyking during its initial four years, when there was little eruptive activity.

The deformation pattern associated with the Ethiopian events[1] suggests that there is a strong vertical variation in the mechanisms that caused them. Faulting seems to have occurred only in the shallowest crust down to a depth of around 2 km, and dyking only in the mid-crust. There is no evidence that the dyke extends below 9 km, indicating that continual ductile deformation processes must prevent the accumulation of tensional stress in this area. A lesson from Iceland is that a rifting episode might consist of many dyking events with an overall duration determined by the period of the magma inflow. More dyking and eruptions might therefore follow in Ethiopia if magma continues to flow to shallower levels. ■

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only a small amount of magma to reach the surface. Continental break-up starts with normal faulting processes and the formation of characteristic 'grabens', where land sinks down between parallel fault systems as the plates on either side diverge (the Great Rift Valley of eastern Africa, of which the Afar rift is part, is a classic example of such a sunken tract of land). Mantle rock, displaced as a graben forms, moves towards the surface, where the lower pressure causes its partial melting. The resulting generation of magma later leads to the onset of voluminous volcanic eruptions[3].

But the new observations imply that many grabens and single faults, even at continental rifts, might reflect dyke-induced faulting[4,5], and might form and evolve through repeated events such as those that occurred in Ethiopia in 2005. An intermediate stage in continental rifting can be envisaged, when melt has begun to be generated in the mantle, but is produced in limited quantities so that most of it is captured inside the extending crust. This period will be dominated by dyking, but characterized by few eruptions.

Another argument for dyking causing early injection of magma into the crust during continental break-up is that it requires less force to dilate brittle crust by upwelling magma than by the slippage of plates in faulting. A stress of some 65 megapascals is needed to initiate slip on a normal fault at a depth of 5 km (ref. 6). In contrast, magma in contact with stretched crust will lead to hydraulic fracturing when

the excess pressure of the magma is about as large as the tensile strength of the crust. This has been inferred to be 1–6 MPa for oceanic crust in Iceland[7]. Thus, any flow of magma into the crust could cause rifting long before the crust is stretched to the degree required for a conventional faulting event.

The study of this rifting episode in Ethiopia increases our understanding of similar events that are taking place on mid-ocean ridges[8], or where these are exposed on land in Iceland and in Djibouti on the Horn of Africa, where the

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ECOLOGY

Asymmetry and stability

Robert D. Holt

Ecological communities are dauntingly complex. Nonetheless, ecologists gallantly persevere in eliciting insights about the factors that govern the behaviour and persistence of these messy, tangled webs.

The concept of symmetry is a guiding principle in much of science, ranging from fundamental physics[1], to analyses of sex-ratio evolution[2], to the dynamics of persistent populations[3]. Yet many phenomena reflect the action of strong asymmetries, including ageing[4], the evolution of species' niches[5], and even the grand sweep of organic and human

history[6,7]. On page 265 of this issue, Rooney *et al.*[8] grapple with the problem of understanding the stability of complex food webs, and argue that strong asymmetries in energy flow and interaction strengths may be key determinants of ecological stability. The word 'stability' has many meanings, but in this context it refers to the capacity of a system

Figure 1 | Top predator. The yellow garden spider (*Argiope aurantia*) is common on the fringes of ponds in northern Florida. Its prey include terrestrial insects such as grasshoppers and crickets, which are sustained by terrestrial vegetation and detritus, and aquatic insects such as caddisflies and damselflies, which when immature live in ponds and so are ultimately sustained by aquatic plant life. Several distinct flows of energy and nutrients are thus merged in the diet of this generalist predator, which is an example of the kind of top predator considered by Rooney *et al.*[8] to be a vital link among different food-web channels.

to recover from perturbations in species abundances.

Ecological communities are among the most complex entities studied by scientists, as they are composed of thousands of species with many distinct lifestyles, interacting in a myriad of ways. Understanding the relationship between the complexity and diversity of ecological systems, and their stability and persistence, is a perennial challenge in ecology. The conventional view that 'diversity begets stability' was overturned by the seminal work of Robert May[9] in the early 1970s. May demonstrated mathematically that increasing the diversity and connectedness of randomly assembled model food webs typically decreased their stability. So if complexity is to enhance ecosystem stability in real food webs, it must emerge from particular structural features of ecological systems.

The authors[8] weave together a survey of empirical studies of food-web energetics with theoretical arguments to suggest that a particular pattern of energy flow found in many food webs may contribute strongly towards stability. At their base, many food webs consist of groups of species that use distinct sources of energy and nutrients. For instance, a lake food web may be sustained by both phytoplankton (which create biomass via photosynthesis) and microbial decomposers (which consume detritus washing into the lake). Phytoplankton and decomposers are very different potential resources for consumers, so organisms in the lower trophic ranks tend to be specialized. In effect, there are distinct 'channels' for inputs of energy and materials into the biota of the lake.

But as one ascends the food web, these channels begin to merge, so a predatory fish such as the lake trout might be sustained ultimately by both phytoplankton production and detritivory.

Rooney *et al.*[8] examine published food-web data from a wide range of aquatic and terrestrial ecosystems, such as marine upwelling regions, estuaries, and agricultural and forest soils. They conclude that the pattern of channels that are distinct at the base of the food web and fuse as energy percolates up the web is widely observed. Top consumers thus integrate a broad base of alternative energy sources (Fig. 1). Crucially, the authors also observe that the different channels are not equally important, but typically exhibit strong asymmetry, with considerably more resources flowing through one channel than through others, but without complete dominance by any particular channel.

The organisms that define these distinct resource channels differ in properties such as body size, generation length and accessibility for higher consumers. These organismal traits have dynamical consequences for the food web as a whole. The authors relate a principal ecosystem concept (turnover rate, which determines how long a given individual takes on average to be replaced) to a principal community concept (interaction strength, which governs how much one species changes in abundance following a change in another's abundance). They suggest that faster channels on average reflect strong interactions, and slow channels, weaker interactions.

This in turn influences the timescale over which the channels in isolation would respond to disturbance. This difference in response

times means that a predator using both fast and slow channels enjoys a more dependable prey base than predators specialized to just one or the other. But there are more subtle implications of coupling channels that emerge from a theoretical study of a model of linked food chains. Assessing the response of the model to both small and large perturbations, Rooney *et al.*[8] show that, in general, asymmetry in the amount of energy flowing through the two levels, and in the pattern of predator attacks, promotes the most stable food webs. They suggest that this is because the simultaneous presence of slow and fast channels prevents dramatic overshoots following large perturbations, while also permitting rapid recovery.

Thus, the asymmetric patterns that the authors document in natural food webs are also the very kinds of asymmetry that promote stability and resilience in theoretical models. There are, of course, many questions that one can pose about the generality of these results. Most of the empirical studies included in the analysis involve highly aggregated data, and the authors' model in essence describes the dynamics of just five interacting species. Including additional species and more complex assumptions about individual behaviour and interspecific interactions can lead to surprises in ecological models[10], and it seems likely that the effects emphasized by the authors could be obscured by other factors in some systems.

Nonetheless, Rooney *et al.*[8] provide an innovative empirical and theoretical contribution to this central ecological problem of identifying potentially key structural features of food webs that promote persistence. As the authors note, human impacts ranging from overharvesting to eutrophication have the effect of reducing the importance of top predators, and effectively homogenizing the energy channels, thus endangering the stability of natural ecosystems. Symmetry is elegant, and often desired in art, human affairs and the formulation of some fundamental theories in science. But in the messy, tangled web of ecological systems, a fair dose of asymmetry may be required to prevent these systems from self-destructing. ■

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