

The ocean is thus best viewed as a mechanically driven fluid engine, capable of importing, exporting, and transporting vast quantities of heat and freshwater. Although of very great climate influence, this transport is a nearly passive consequence of the mechanical machinery. When Stommel (10) first introduced the term "thermohaline circulation" in a box model, he explicitly provided a source of mechanical energy in the form of mixing devices. These devices disappeared in subsequent discussions and extensions of this influential model.

For past or future climates, the quantity of first-order importance is the nature of the wind field. It not only shifts the near-surface wind-driven components of the mass flux, but also changes the turbulence at depth; this turbulence appears to control the deep stratification. The wind field will also, in

large part, determine the regions of convective sinking and of the resulting 3D water properties. Fluxes and net exports of properties such as heat and carbon are determined by both the mass flux and spatial distribution of the property, and not by either alone.

Tidal motions were different in the past than they are today, owing to lower sea level during glacial epochs, and moving continental geometry in the more remote past. The consequent shifts in tidal flow can result in qualitative changes in the oceanic mixing rates, and hence in the mass and consequent property fluxes.

The term "thermohaline circulation" should be reserved for the separate circulations of heat and salt, and not conflated into one vague circulation with unknown or impossible energetics. No shortcut exists for determining property fluxes from

the mass circulation without knowledge of the corresponding property distribution.

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PERSPECTIVES: CONSERVATION BIOLOGY

Predictive Ecology to the Rescue?

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The recently released *Red List of Threatened Species*, compiled by the World Conservation Union, lists one quarter of the world's mammalian species as threatened with extinction, along with 12% of birds and between 20 and 30% of fishes, reptiles, and amphibians (1). The *Plan of Implementation* approved at the World Summit on the Environment held in Johannesburg in September affirms the goal of achieving by 2010 a significant reduction in the rate of biodiversity loss. What role can conservation biologists play in addressing this biodiversity crisis, and where are we to begin? There is no point in planning long-term, detailed investigations into the ecology of every species that may be under threat. We have neither the time nor the resources to do this for the vast majority of species that we know to be endangered, let alone the countless other organisms whose conservation status has not yet been assessed. We need simple ecological rules of thumb that can be applied broadly to help prioritize conser-



Aliens and altered landscapes. (Top) A round goby fish (*Neogobius melanostomus*) and a zebra mussel (*Dreissena polymorpha*). Both species originate from the Black Sea and Caspian basins and are thought to have been introduced to the Great Lakes of North America from the ballast waters discharged by trans-Atlantic ships. Both are prolific breeders, insatiable feeders, and aggressive competitors for space. These characteristics have put these two species at a competitive advantage relative to native species. **(Bottom)** The Taita Hills forest ecosystem of southeast Kenya is part of the Eastern Arc biodiversity hotspot, which is home to a wide variety of endemic plants and animals. Years of deforestation for conversion to agriculture have transformed the formerly dense forest into a patchwork of more or less degraded fragments.



vation action and funding. Two papers in this issue, by Kolar and Lodge on page 1233 (2) and by Lens *et al.* on page 1236 (3), demonstrate that such rules of thumb may well exist.

Kolar and Lodge (2) tackle the issue of introduced species that rank as a major cause

of extinction threat in many parts of the world. Why do some introduced species flourish whereas others fail? Species that are ecological generalists (that is, they tolerate a broad range of environmental conditions) and produce many offspring quickly are expected to be robust invaders (4). Yet, there have been few attempts to test this hypothesis.

Kolar and Lodge take on the challenge with their investigation of alien fish species in the Great Lakes of North America (see the figure). Construction of canals in the 19th century and of the St. Lawrence Seaway some 50 years ago inadvertently opened a floodgate of alien species introductions into the Great Lakes. Species such as the sea lamprey (*Petromyzon marinus*) and, more recently, the zebra mussel (*Dreissena polymorpha*) have wrought economic and ecological havoc. Clearly, the ability to predict the establishment and impact of such species before their introduction could have led to stricter control measures.

These investigators compared the characteristics of alien fish species that became established or failed to spread, that spread quickly or slowly, and that became a nuisance or had little ecological or economic impact. As expected, at all stages of the invasion process successful species tended to have wide

temperature or salinity tolerance and rapid life histories (although the speed at which they spread was, surprisingly, related to slower growth rates). Armed with these results, the authors predicted the likelihood of invasion of fish species native to the Black Sea, Caspian Sea, and surrounding watersheds,

which are the source of a large number of alien species introduced into the Great Lakes. Their model pinpointed 22 fish species that show the characteristics of good invaders, of which five (including the European perch, *Perca fluviatilis*, and Eurasian minnow, *Phoxinus phoxinus*) are predicted to become nuisance species. The ecosystem impacts of further introductions to the Great Lakes are difficult to assess, but given the clear potential for these to happen, measures should be put in place immediately to prevent them. Such measures could include treatment of ballast waters discharged by ships and prohibiting the importation of high-risk species for the aquaculture, pet, and live-bait industries.

In the second study, a similar predictive approach is taken by Lens and colleagues (3), who examine the persistence of species in fragmented habitats. This time, the focal taxon is birds and the ecosystem is the Taita Hills forest of southeast Kenya, which is part of the Eastern Arc biodiversity hotspot (see the figure). These high hills were once blanketed by a continuous cover of humid forest, but after years of deforestation for conversion to agriculture, only 12 fragments remain, the largest of which spans an area of only 179 ha. Which species are likely to persist and which are likely to be lost when the habitat is fragmented to such an extent?

Lens *et al.* show that the more mobile bird species fare best, but equally important is the sensitivity of species to the environmental deterioration that occurs *within* frag-

ments. Degradation inside forest patches results, for example, from selective removal of mature trees for building materials and introduction of exotic species for small-scale plantations. The index of sensitivity was based on a clever comparison between the asymmetry in left and right tarsus lengths of birds living in the most degraded forest fragment, and that of museum specimens collected several decades before habitat deterioration. The larger the departure from historical asymmetry, the more sensitive is the species to habitat change. This link is based on previous studies showing that the bilateral traits of birds living in more degraded habitats are more asymmetric (5), and that birds with asymmetric characteristics die at an increased rate (6).

These two seemingly disparate studies have two remarkable features in common. The first is that the best models that the authors devised to explain their respective problems incorporated very few parameters (three or four in the case of Kolar and Lodge; only two in the case of Lens *et al.*). The second is that these simple models explain a huge amount of the variation in the respective data sets (more than 80% in both cases). This gives the models great predictive power, but their usefulness will depend on their general applicability and on how easily the necessary parameters can be measured. This is where the studies differ. Kolar and Lodge were able to extract all of their information from published literature or from

questionnaires. By contrast, the two parameters in Lens *et al.*'s model required 6 years of labor-intensive fieldwork and the availability of museum specimens to compare levels of fluctuating asymmetry. In addition, there is a good chance that Kolar and Lodge's predictions will apply broadly to aquatic ecosystems, and unfortunately, there are numerous waterbodies riddled with introduced fish that can be used as test cases. On the other hand, the conclusions of Lens *et al.* may be more system-specific. The Taita Hills forest fragments are still close enough together to allow dispersal, giving mobile species an advantage. However, mobility will be irrelevant when fragments are too far apart. How far is too far can be predicted by metapopulation theory (7). Together, these studies show the value of using ecological theory to guide the search for general rules in conservation biology, and suggest that complex problems may sometimes have simple explanations.

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PERSPECTIVES: MATERIALS SCIENCE

Talking Ceramics

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In the last three decades, telecommunications have been completely transformed. Devices such as cell phones are now so common that many consumers are forgoing the hard-wired versions altogether.

This remarkable change could not have taken place without several key historical events, such as Marconi's first wireless transmission across the Atlantic Ocean in 1901 and the discovery of the transistor almost 50 years later (1). Also critical was the discovery of unique ceramic materials that could be used as dielectric resonators and filters to store and transfer microwave communication signals.

Richtmyer coined the term "dielectric resonator" in 1939 (2), when he wrote, "if a long dielectric cylinder were bent into a

ring and the ends joined together, it would guide the waves round and round indefinitely" (see the figure). He concluded that "such an object would act as an electrical resonator," possibly useful in electrical communication, because the resonant frequency would radiate from the resonator through free space, and thus could be detected by other (receiving) devices.

The size of the resonator is inversely related to the dielectric constant, K , of the internal medium. The first versions, which used air as the dielectric ($K \approx 1$), were too large for practical use. Subsequent designs with a ceramic such as TiO_2 ($K \approx 100$) allowed size reduction by a factor of 10. However, they also proved impractical because the resonant frequency, and hence the communication signal, were strongly temperature dependent and would drift as operational temperatures varied (for example, on hot versus cold days).

This technological barrier was overcome in the 1970s by the discovery of $\text{Ba}_2\text{Ti}_9\text{O}_{20}$ -based ceramics (3, 4), which have the required set of properties: a high dielectric constant, low dielectric loss (conversion of signal to heat, which broadens the signal), and temperature-stable resonant frequency (5–8). In the next two decades, cellular base station technologies proliferated (see the second figure), and the volume and weight of handheld devices plummeted.

Today, dielectric ceramics are commercially important as enabling materials for resonators, filters, and other key components in microwave communications systems. The global market for the ceramics is on the order of \$400 million; the markets for the resulting devices and components, and for the end-user systems, are ~10 and ~100 times that size, respectively.

Despite their technical importance and widespread use, very few ceramic materials are known that meet the stringent property requirements (5–7) imposed by the operating frequency, required power levels, and type of application (base station or handheld device). Only two ceramic materials are optimized for 900-MHz base sta-

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