

scious processing in humans. Moreover, several studies have reported residual local and specific brain activation patterns in vegetative state patients, whereas long-range neural integration observed during conscious processing was lacking (4, 5). Nevertheless, on the basis of their findings, Owen *et al.* argue that the patient in their study was probably conscious of herself and her surroundings during fMRI testing. This hypothesis opens another issue: If this patient is actually conscious, why wouldn't she be able to engage in intentional motor acts, given that she had not suffered functional or structural lesion of the motor pathways?

The debate over whether vegetative state patients can engage in conscious processing is reminiscent of the Turing test in artificial intelligence: Can we distinguish a conscious human from a computer solely on the basis of a question-answer method (6)? Adapting the Turing test to the present debate, we might ask: Can we determine whether a person is conscious solely on the basis of a question-brain activation method? Whereas these questions have stimulated intense philosophical debate about artificial intelligence, most cognitive

neuroscientists have adopted a more naturalistic approach. Consciousness is univocally probed in humans through the subject's report of his or her own mental states. A subject who reports, "I read the word consciousness on this page," can be considered as conscious (7). The ability to report one's own mental state is the fundamental property of consciousness.

Owen *et al.* did not directly collect such a subjective report. When conscious reporting is not possible, an alternative solution is to examine the three other psychological attributes of conscious processing: (i) active maintenance of mental representations; (ii) strategical processing; and (iii) spontaneous intentional behavior (8). Clearly, one of the most impressive aspects of the work by Owen *et al.* is the demonstration that activation of task-related neural networks is actively maintained. During each experimental task, instructions were delivered only once, and the corresponding neural network remained activated throughout the entire 30-s period. In contrast, unconscious mental representations observed in many clinical and experimental contexts are fleeting, lasting a few seconds or less (9–11).

Though not totally convincing on the issue of consciousness, the Owen *et al.* work paves the way for future functional brain-imaging studies on comatose and vegetative state patients. One can imagine probing each of the psychological properties of conscious processing listed above, and even trying to collect subjective reports by modifying the experimental paradigm.

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#### ECOLOGY

## How Does Climate Change Affect Biodiversity?

Miguel B. Araújo and Carsten Rahbek

Over the past 100 years, Earth's climate has become warmer and precipitation regimes have changed. Can biologists predict the effects of these changes on the distributions of species?

Conservation strategies for managing biodiversity have traditionally assumed that species distributions change relatively slowly, unless they are directly affected by human activities. However, there is a growing consensus that these strategies must anticipate the impacts of climate change (1, 2). Conservationists must therefore assess both current and future distributions of species. Numerous new bioclimatic models estimate relationships between the distributions of species and climate. However,

the decision of which model to use has generally been ad hoc, and there is little consensus regarding the relative performance of these models.

Bioclimatic modeling has been driven by a pragmatic desire to obtain results that are useful for biodiversity management (3, 4). The models are based on some problematic ecological assumptions—for example, that species distribution and assemblages are in a constant steady-state relationship with contemporary climate—that, despite being clearly acknowledged (5), remain unresolved. However, there has been even less emphasis on understanding which models best predict species distributions and why.

The proponents and architects of some of the most prominent bioclimatic models recently joined forces to test the predictive uncertainties of their models and to identify the techniques best suited for modeling current species distributions. Elith *et al.* have now published the first results in *Ecography* (6). Sixteen models were tested on climate

The most recent and complex bioclimate models excel at describing species' current distributions. Yet, it is unclear which models will best predict how climate change will affect their future distributions.

and species distribution data from five continental regions. In contrast to many previous studies, data for testing the models were collected independently.

The models with the best performance were the most recent and complex ones and fell into two groups: machine-learning programs that seek to obtain a stable selection of predictors from a larger range of alternatives, and community models that simultaneously analyze all species in relation to environmental parameters and then calibrate model coefficients for individual species. In contrast, some of the most widely used models for modeling species distributions, such as GARP (which uses a genetic algorithm) and BIOCLIM (which uses an envelope approach), performed poorly under the criteria used to evaluate them.

One critical question is whether models that can successfully predict current species distributions also provide robust predictions of future distributions under climate change. (This question is not addressed by Elith *et al.*,

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who focus on current distributions.) Different bioclimatic models can produce highly variable predictions of species-range shifts (7–11), and there is a poor correlation between a model's ability to fit present and future distributions (12). For example, Pearson *et al.* (9) applied nine bioclimatic models to predict the distributions of four South African plants under current and future climates. Predicted distribution changes varied from 92% loss to 322% gain for one species; similar variability was recorded for the other species. In another study, observed and predicted changes in the distributions of British breeding birds differed markedly for 90% of the 116 birds modeled (see the figure) (8).

Evaluating model performance under climate change requires a paradigm shift, because there are no data against which pre-

dictions of future ranges can be tested (12). One way to overcome this problem is to make use of backward predictions, or “hindcasting.” Here, models are calibrated with current species-climate relationships and are then tested with reconstructed species distributions from the fossil record. This approach has been used to test whether climatic requirements of species remain stable over time (13, 14). However, hindcasting is only feasible for a few species and regions for which a good fossil record is available.

The predictive ability of models can also be tested through “space-for-time” substitution. Here, bioclimatic models are calibrated with data from one region, and predictions are tested with distributions of species from other regions. Randin *et al.* recently illustrated the principle by predicting plant species distribu-

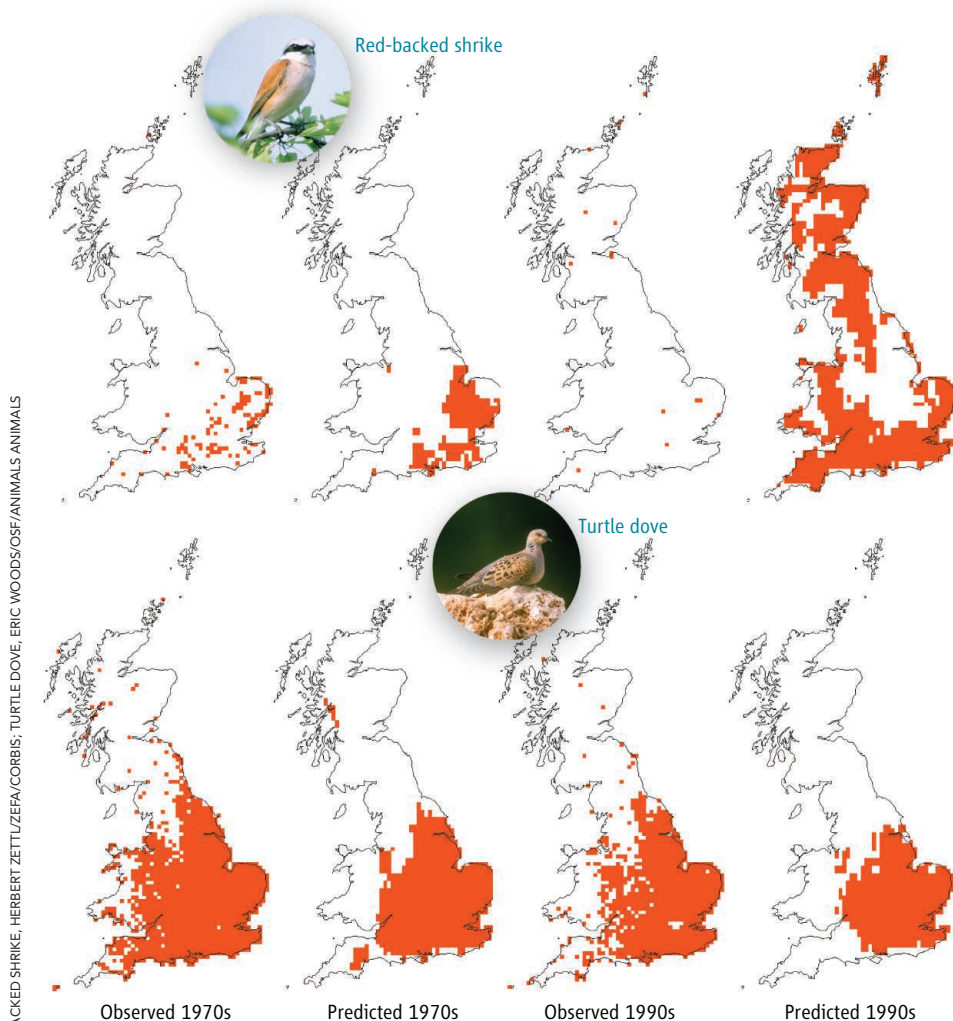
tions in the Austrian Alps based on knowledge of species-climate relationships in the Swiss Alps and vice versa (15). They found that predictions from generalized linear models (which impose a theoretical response curve) were more easily transferable in space and time than generalized additive models (which produce data-driven response curves). However, the latter yielded more precise predictions in the regions where the models had been calibrated.

Do data-driven, machine-learning, and community models provide more precise predictions of species distributions in a given region because they overfit the data? Does model precision come at the expense of generality, that is, the ability to predict species distributions in different regions or times? And do theory-driven response curves improve the generality of models? The results of the two studies (6, 15) call for a second generation of studies to test predictions of bioclimatic models under climate change.

Predictions of future distributions of species from bioclimatic models may fail because of uncertain predictions of local climate change, inaccurate estimates of the climatic tolerance of species, and unforeseen evolutionary changes in populations (16). We will never be able to predict the future with accuracy, but we need a strategy for using existing knowledge and bioclimatic modeling to improve understanding of the likely effects of future climate on biodiversity.

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**A mixed picture of model performance.** Observed and predicted distributions of the red-backed shrike (*Lanius collurio*) and turtle dove (*Streptopelia turtur*) in Britain. Bioclimatic models predict the distributions in the 1970s reasonably well, but fail to predict the contraction of the range of the red-backed shrikes in the 1990s. However, the contraction of the range of the turtle dove is successfully predicted by models. Maps were produced with data and generalized linear models from (8).

PHOTO CREDITS: RED-BACKED SHRIKE, HERBERT ZETTLZEFA/CORBIS; TURTLE DOVE, ERIC WOODS/OSF/ANIMALS ANIMALS

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