tistical analysis on normalized compiled data from all the experiments reveals that both the difference between low pH and median pH and that between low pH and high pH are significant ($P = 0.044$ and $P = 0.005$, respectively; t test, two-tailed distribution). Because we know that pH variations in this range have no effect on the Fe uptake capabilities of *T. weissflogii*, the observed decrease in Fe uptake rate is presumably due to a change in the chemical speciation of Fe with pH. On average, the Fe uptake rate decreased by about 10 to 20% from the high-pH (~8.4) to the low-pH (~7.8) conditions in the experiments we conducted, reflecting presumably the acid-base chemistry of the mixture of functional groups responsible for Fe chelation in the various water samples used for the experiments. It would appear from the modest effect of acidification on Fe uptake rates that little of the iron was bound to carboxylic acid moieties in our field samples. The only published experiments on the effect of pH on iron speciation in seawater show that, in a sample of surface water from the North Sea, Fe′ decreased with decreasing pH (*27*), which is consistent with our observations. Those results also imply that the effectiveness of natural ligands in maintaining Fe in solution might be increased at low pH and may result in a slower Fe loss via the formation of Fe oxyhydroxide precipitates. The very low ambient biomass in Sargasso Sea samples and the high concentrations of suspended particulate material in unfiltered New Jersey samples precluded Fe uptake experiments with the ambient phytoplankton populations.

The ongoing increase in atmospheric CO_2 will have many indirect and direct effects on the physics, chemistry, and biology of the ocean. Our laboratory and field results show that one such effect is a decrease in the bioavailability of dissolved Fe caused by the acidification of the water. This effect should be particularly important in areas where the major source of Fe at the surface is from the dissolved Fe in deep waters (*28*). In areas where particulate Fe inputs are important (*29*), this effect may be partially compensated by the increased effectiveness of some chelators in dissolving Fe from oxyhydroxides and/or by enhancing the photo-induced redox cycle of Fe (*30*). We have found so far no evidence that an increase in P_{CO_2} above present-day values results in a lower Fe requirement. It thus seems likely that, unless Fe inputs to surface seawater increase as a result of global change, the net result of seawater acidification should be an increase in the Fe-stress of the phytoplankton in many areas of the oceans.

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Gradual Adaptation Toward a Range-Expansion Phenotype Initiated the Global Radiation of Toads

Ines Van Bocxlaer,[1] Simon P. Loader,[2] Kim Roelants,[1] S. D. Biju,[3] Michele Menegon,[4] Franky Bossuyt[1]*

Recent studies have identified range expansion as a potential driver of speciation. Yet it remains poorly understood how, under identical extrinsic settings, differential tendencies for geographic movement of taxa originate and subsequently affect diversification. We identified multiple traits that predict large distributional ranges in extant species of toads (Bufonidae) and used statistical methods to define and phylogenetically reconstruct an optimal range-expansion phenotype. Our results indicate that lineage-specific range-shifting abilities increased through an accumulation of adaptive traits that culminated in such a phenotype. This initiated the episode of global colonization and triggered the major radiation of toads. Evolution toward a range-expansion phenotype might be crucial to understanding both ancient widespread radiations and the evolutionary background of contemporary invasive species such as the cane toad.

Bursts of species diversification have played a central role in shaping current biodiversity patterns across the world (*1*). Such periods of accelerated speciation have been typically linked to adaptive radiations, whereby ecological differentiation happens in a group of related sympatric species (*2*). However, recent studies have suggested an important role for range expansion in promoting speciation rates (*3, 4*), which raises the question of why, under identical extrinsic settings (e.g., land bridges, climate change), some lineages have dispersed while others diversified in situ (*5*). Transferring this notion from ecological to historical biogeography is difficult because of the lack of lineage-specific information on traits promoting range expansion (*3, 4, 6, 7*). We identified such traits in extant toads (Bufonidae) through their present-day correlation with species distribution ranges. Evolutionary reconstructions in a comprehensive phylogenetic, biogeographic, and temporal framework provide a means to elucidate the evolutionary history of these traits and their consequences for speciation in this group.

Toads attained a subcosmopolitan distribution in a very short time frame (*8, 9*), and the

500 known species show an interesting diversity in larval and adult adaptations on each continent (Fig. 1, A and B). Additionally, whereas some bufonids are endemic to a small area and are extremely vulnerable (e.g., harlequin toads) (10), others (e.g., the cane toad) are notorious for their ability to adapt and expand their range at an exceptional pace (11). These differences

[1]Biology Department, Amphibian Evolution Lab, Unit of Ecology and Systematics, Vrije Universiteit Brussel, Pleinlaan 2, B-1050 Brussels, Belgium. [2]Department of Environmental Sciences, Section of Biogeography, University of Basel, 4056 Basel, Switzerland. [3]Systematics Lab, Centre for Environmental Management of Degraded Ecosystems (CEMDE), School of Environmental Studies, University of Delhi, Delhi 110 007, India. [4]Sezione di Zoologia dei Vertebrati, Museo Tridentino di Scienze Naturali, Via Calepina 14, I–38100 Trento, Italy.

*To whom correspondence should be addressed. E-mail: fbossuyt@vub.ac.be

provide an excellent basis for a comparative evolutionary study of the influence of intrinsic, range expansion–promoting traits on speciation rates.
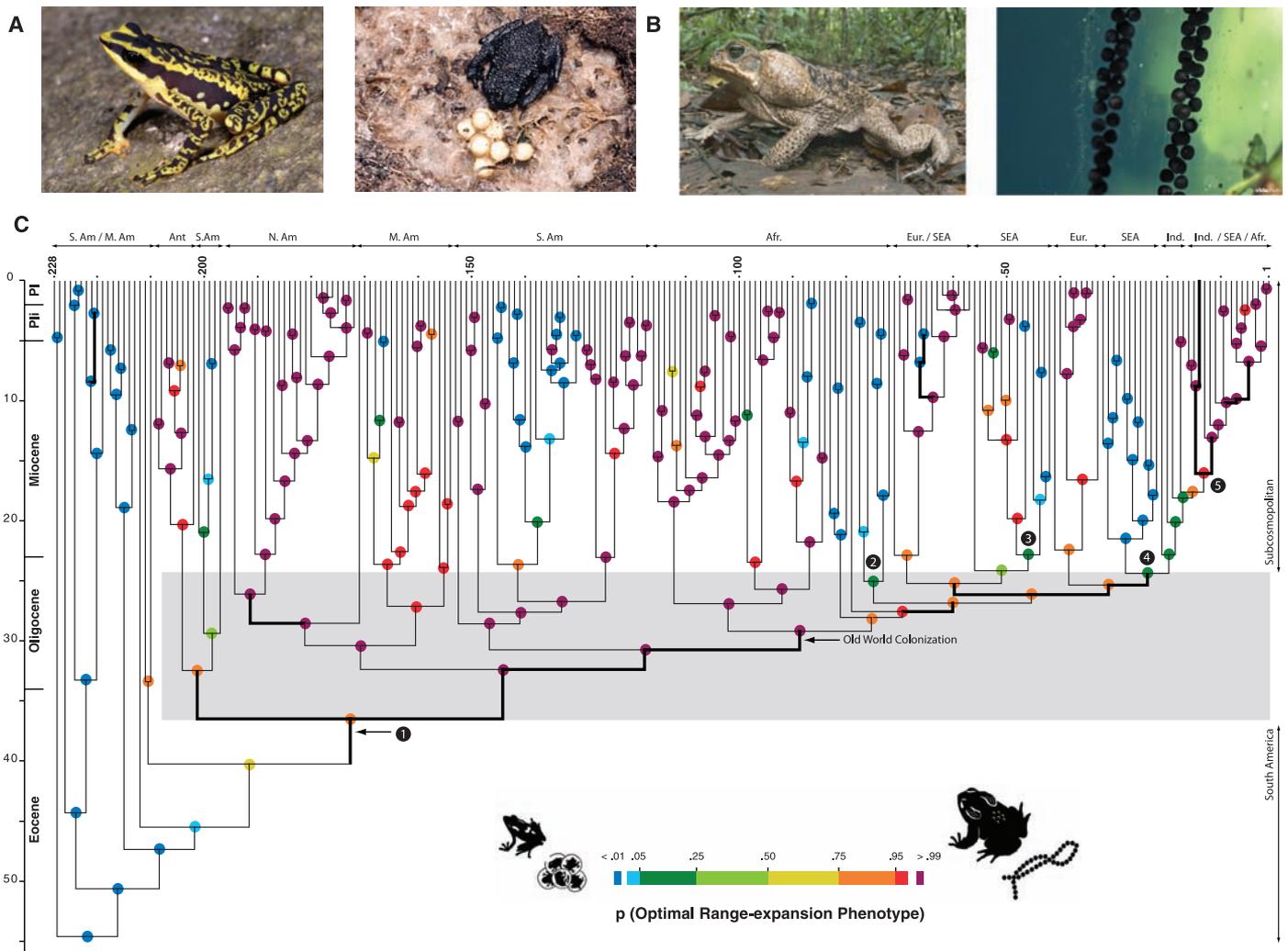
To search for traits that can be directly or indirectly linked to such differences in extant species, we used phylogenetically controlled statistical tests that check for a correlation with current distribution ranges as a proxy for range-expansion ability (12). We constructed a data set of 228 taxa (~43% of bufonid species diversity) sampled from all over their distribution range. Maximum likelihood and Bayesian analyses yielded a time-calibrated tree that is largely congruent with previous studies. Subsequent biogeographical reconstructions confirm that range expansion started in South America and rapidly resulted in colonization of the major continents (8) (Fig. 1C, gray box). We identified seven life history traits that, on the basis of their documented functions, are candidate promoters of range-expansion ability (Table 1) and used character evolution simulations to ascertain that none of the observed correlations with present-day species distribution areas were caused by phylogenetic dependence (12).

Our data indicate a significantly larger distribution for species whose adults are not dependent on the constant availability of water bodies, high air humidity levels, or damp substrates, relative to species whose adults are dependent on such conditions ($P < 0.001$). The former may have diverse cutaneous adaptations that allow them to disperse through a variety of habitats (13). Species with parotoid glands (parotoids) show significantly larger distribution areas as well ($P < 0.001$). These glands secrete an array of molecules that are poisonous to many animals and are one of the components

Fig. 1. Range-expansion ability in toads. (**A**) Examples of species at the lower end of the spectrum. Left: *Atelopus cruciger*, adult, a riparian species. Right: *Oreophrynella nigra* next to a small egg clutch on land. (**B**) Examples of species at the higher end of the spectrum. Left: *Rhinella marina*, the cane toad, is infamous for its invasion of the Australian continent. Right: Strings that contain thousands of eggs in *Bufo bufo*. (**C**) Molecular time scale for 228 taxa. Colored dots indicate the estimated probabilities of the ORP (index 2, see text) based on the five adult and developmental traits (12) indicated with an asterisk in Table 1. The gray box indicates the major period of global colonization. Darker branches were reconstructed as dispersal events by Lagrange analysis (28). The estimated probabilities of the ORP show a gradual increase toward the dispersing lineages (nodes 1 and 5) and a decrease after the major period of global colonization (nodes 2, 3, and 4). Drawings symbolize species at the lower and higher ends of the range-expansion ability spectrum.

contributing to the success of the cane toad invasion in Australia (*14*). Furthermore, parotoids have large granular alveoli holding a secretion that contains highly hydrophilous glycosaminoglycans, allowing the retention of large quantities of water during the dry season (*15*). Our data also indicate a significant correlation with the presence of inguinal fat bodies ($P < 0.001$), fat storage organs important for providing supplementary energy when resources are limited (*16*). Finally, species with a large adult size (snout-vent length > 50 mm in males) show a significantly larger distribution than smaller species ($P < 0.001$). It has been argued that relative water loss is minimal with small surface-to-volume ratios, as observed in large animals (*13*), and that water retention is optimal with large relative bladder size, as observed in *Bufo* species (*17, 18*).

We also identified three traits in reproduction and development that show significant correlation with modern species' distribution ranges (Table 1). Relative to species that are restricted to specialized oviposition, species laying their eggs in various kinds of water bodies have significantly larger ranges ($P < 0.001$). Such species are capable of laying eggs in temporal water bodies—that is, whenever rainfall conditions become favorable—and can more easily disperse and reproduce in harsh habitats (*13*). Comparison of larval feeding modes shows that species with exotrophous larvae (which take food from the environment) also have a larger distribution than species with endotrophous ones (which obtain food from maternal sources of energy, requiring a more costly parental investment) (*17*) ($P < 0.001$). Finally, egg clutch size is extremely variable, ranging from 45,000 eggs in *Anaxyrus cognatus* to only five in *Pelophryne* species (*19, 20*), and our analyses indicate larger distribution areas for species with large clutch sizes ($P < 0.001$).

The strong correlation of these traits with present-day distribution ranges identifies them as plausible indicators of range-expansion ability in toads (i.e., a large present distribution range implicates a past episode of range expansion). As a consequence, their combined presence is expected to constitute an optimal range-expansion phenotype (ORP), whereas other combinations of presence or absence of these traits approximate the ORP to a lesser degree. This rationale was used to reconstruct variations in range-expansion ability throughout toad evolutionary history.

Reconstructions of individual traits (*12*) generally indicated high probabilities for range shift–promoting character states at periods of transcontinental colonization (Fig. 1C). We used two indices to summarize the evolutionary history of these traits for each ancestral node: (i) the number of range expansion–promoting traits that had a high (>95%) probability of being present, and (ii) the product of the probabilities for individual character states, which indicates the probability of reflecting the ORP as a whole (Fig. 1C). Both indices show a gradual increase along basal branches of the bufonid radiation predating the period of global colonization.

Maximal scores for both indices are reached at the branches of the first transcontinental dispersal event out of South America (Fig. 1C, branch 1) and subsequent global colonization (Fig. 1C, gray box). After spreading across the Old World, several lineages on different continents independently attained more specialized ecomorphs, as reflected by parallel decreases of the indices in Africa, Southeast Asia, and the Indian subcontinent (Fig. 1C, nodes 2, 3, and 4, respectively). Notably, we estimate a second major increase in both indices along the branches of a widespread (i.e., Indian subcontinent, Southeast Asia, and northern Africa) clade (Fig. 1C, node 5) that evolved from ancestors endemic to the Indian

Western Ghats and Sri Lanka (Fig. 1C, between nodes 4 and 5) (*9*). The bufonid ORP matches the typical *Bufo* morphology (i.e., a relatively large terrestrial toad with glandular skin and large parotoids). This morphology is still widespread among modern species, and the fact that distantly related species often look very similar has confounded taxonomy in this family for decades.

To evaluate whether the increase in range-expansion ability led to increased speciation, we inferred speciation rates under various models of net diversification (i.e., with relative extinction rate ranging from zero to an extremely high value). Rate-through-time plots of net diversification suggest, under any model, an acceleration of bufonid speciation during the period of global colonization (Fig. 2, gray box). This acceleration immediately followed the rise of the ORP, a pattern that is robust against uncertainties in phylogenetic reconstruction and divergence time estimation (*12*). Furthermore, the subsequent decrease in net diversification follows the arrival of toads on each of the continents, indicating that in situ speciation was generally slower than range expansion–correlated speciation. Biogeographic reconstructions distinguishing between speciation within a single continent and speciation after an intercontinental range expansion show that the latter makes up 43% of the total number of nodes during the radiation (versus 0% before and 4% after this episode). This suggests that range expansion itself was an important driver of diversification in bufonids.
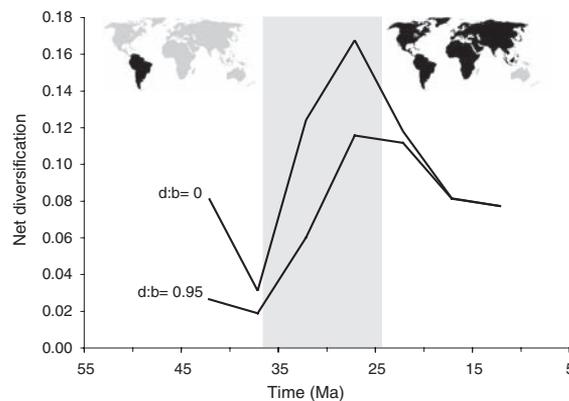
Fig. 2. Rate-through-time plot of net diversification for successive 5-million-year intervals for bufonids (Ma, million years ago). The gray box refers to the period of global colonization.

Table 1. Traits that are promoters of range expansion, as indicated by statistical tests (i.e., $P < 0.001$ for U test and test of phylogenetic independence). Characters with an asterisk were used for index calculations.

Traits	Context
Adults	
(Semi-)terrestrial adult niche (according to IUCN data)*	No dependency on constant water or humidity
Large body size	Higher relative water storage ability in bladder
Presence of parotoid glands*	Enhanced toxicity and rehydration ability
Presence of inguinal fat bodies*	Extra energy reserve (extra fat storage ability)
Reproduction and development	
Aquatic, opportunistic oviposition site*	Ability to use all kinds of water bodies, including those in harsh habitats
Large clutch size	Typical feature of r-strategy
Exotrophous larvae*	Limited maternal investment in larval nutrition

The observed pattern of accelerated speciation shows major differences from classic models of adaptive radiation. In these models, phenotypic changes often coincide with genetic isolation of populations in various ecological niches (ecological speciation). Our study demonstrates that the adaptive origin of phenotypic traits that increased colonization ability happened before the radiation of toads. Our macroevolutionary analyses did not identify major changes during the period of accelerated speciation. Yet, as observed in expanding populations, the process of geographic movement may have further driven evolutionary optimization of traits that promoted range expansion (21, 22). We hypothesize that these reciprocal effects have caused the rapid global colonization of bufonids and produced enhanced genetic drift at the expanding frontier, with consequent high levels of population differentiation and speciation (23–25). If so, toads demonstrate an interesting link between macroevolutionary and microevolutionary processes promoting speciation. Because many species radiations now have large distribution ranges, often covering multiple continents (4, 26, 27), evolutionary shifts in traits promoting range-expansion may have significantly contributed to shaping today's ecosystems. Finally, our reconstruction puts the rapid and destructive expansion of the cane toad in Australia into a macroevolutionary context: The origin of this range-expansion ability appears to be rooted deep in the evolutionary tree of toads and may be a remnant of the period when toads colonized the world.

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Flight Orientation Behaviors Promote Optimal Migration Trajectories in High-Flying Insects

Jason W. Chapman,[1]* Rebecca L. Nesbit,[1,2] Laura E. Burgin,[3,4] Don R. Reynolds,[1,5] Alan D. Smith,[1] Douglas R. Middleton,[3] Jane K. Hill[2]

Many insects undertake long-range seasonal migrations to exploit temporary breeding sites hundreds or thousands of kilometers apart, but the behavioral adaptations that facilitate these movements remain largely unknown. Using entomological radar, we showed that the ability to select seasonally favorable, high-altitude winds is widespread in large day- and night-flying migrants and that insects adopt optimal flight headings that partially correct for crosswind drift, thus maximizing distances traveled. Trajectory analyses show that these behaviors increase migration distances by 40% and decrease the degree of drift from seasonally optimal directions. These flight behaviors match the sophistication of those seen in migrant birds and help explain how high-flying insects migrate successfully between seasonal habitats.

Long-distance transcontinental migrations by animals are well known, but the orientation strategies employed by migrants are poorly understood (1–3). This is particularly true of insects (4), many of which take advantage of airstreams hundreds of meters aloft for rapid transport between seasonal habitats. For example, moths migrate at altitudes where wind speeds greatly exceed the migrants' self-powered airspeeds (5–7), but the extent to which individuals are able to move in favorable directions, and how this is achieved, is not clear (2, 8). In contrast with nocturnal insects, day-flying migrant butterflies are usually assumed to travel close to the ground where wind speeds are slower than the insects' airspeeds (9), although substantial butterfly migration may also occur at high altitudes (10, 11). However, whether high-flying butterflies are still capable of maintaining seasonally beneficial migration trajectories, as they can at ground level

(12–14), is not known. More important, the consequences of these flight behaviors for promoting successful migration have not been examined. We studied flight behavior in a range of high-altitude migrant Lepidoptera and modeled the effects of these behaviors on migration trajectories.

We analyzed data from vertical-looking entomological radars [VLR (15)] in the United Kingdom from 2000 to 2007 (16). Our VLRs record large-scale wind-borne migrations 150 to 1200 m above the ground (fig. S1), involving billions of insects. We focus on Lepidoptera, which predominate in these VLR data (6, 17, 18). Using radar data for >100,000 individual insects collected from 569 separate mass migration "events" (16) in spring and fall, we examined seasonal distributions of migratory displacements and flight headings of four groups of migratory insects [the noctuid moths *Autographa gamma* and *Noctua pronuba* (6, 17, 18); hawkmoths (Sphingidae); and butterflies (16)], which spend the winter

[1]Plant and Invertebrate Ecology Department, Rothamsted Research, Harpenden, Hertfordshire AL5 2JQ, UK. [2]Department of Biology, University of York, Heslington, York YO10 5YW, UK. [3]Met Office, FitzRoy Road, Exeter EX1 3PB, UK. [4]School of Geography, University of Exeter, Exeter, Devon EX4 4RJ, UK. [5]Natural Resources Institute, University of Greenwich, Chatham, Kent ME4 4TB, UK.

*To whom correspondence should be addressed. E-mail: jason.chapman@bbsrc.ac.uk