Flattening of the Rainforest-Savanna Gradient Reduces Adaptive Diversity in a Rainforest Bird in West Africa

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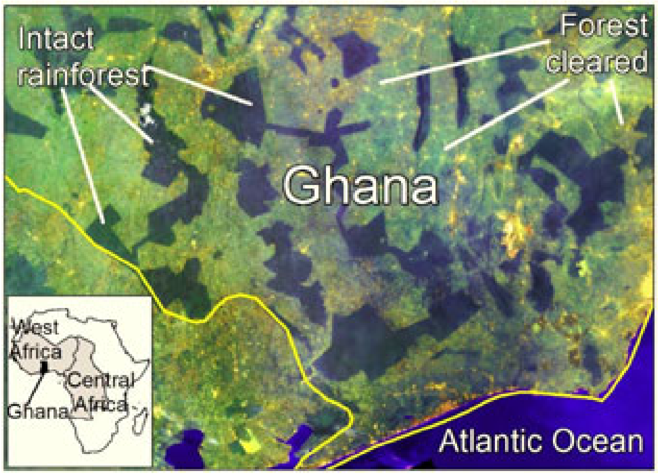


Satellite image of rainforest (dark polygons) and human-altered areas (faded green and yellow) in Ghana, West Africa

Pan over Ghana, in West Africa, with Google Earth, and zoom in. Small, jagged polygons of dark green rainforest float in isolation on a sea of faded green and yellow. Palm oil and banana plantations, patchworks of small-scale agriculture, fire scars from burning, and expanding human settlements are all that remain of a once vast, nearly continuous belt of equatorial rainforest. Scientists and celebrities alike have decried this rainforest loss as well as the species extinctions accompanying it. Yet amidst all of the unfortunate bookkeeping necessitated by species extinctions, the evolutionary consequences of rainforest loss have mostly been overlooked.

But why care? At first glance, one might think that the timescale of evolutionary events is an order of magnitude larger (slower) than the pace of human land conversion, such that short-term attrition should be the focus of conservationists. A recent paper, “Human impacts flatten rainforest-savanna gradient and reduce adaptive diversity in a rainforest bird,” published in *PLoS ONE* by myself, in collaboration with a team of Center for Tropical Research (CTR) scientists and external researchers, suggests that this view is incorrect. The evolutionary consequences of rainforest loss can be profound and may limit the ability of rainforest species to persist in the face of future environmental perturbations such as global climate change.

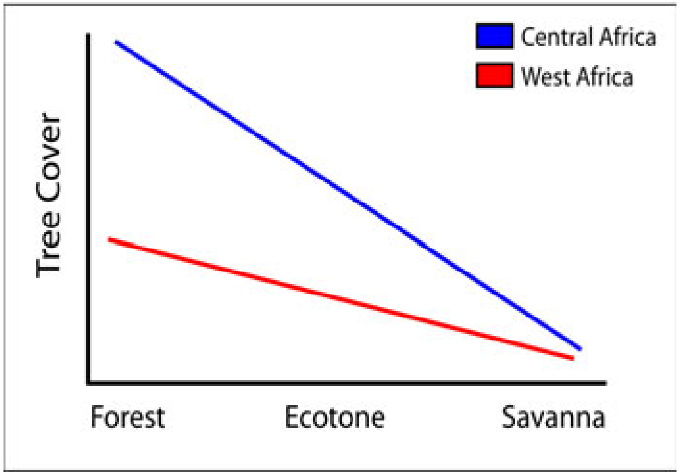
Over the past twenty years, CTR researchers have produced evidence that in rainforests worldwide, for a wide range of taxa, the processes of diversification and speciation take place not only within “biodiversity hotspots,” but also along environmental gradients. Gradients are the observable changes in environmental conditions across a landscape. At different locations along a gradient, individuals of a species are exposed to different environmental conditions. These gradients are characterized not only by the features that comprise them (e.g., temperature, precipitation, and habitat structure), but also by the rate at which these features change between locations, usually described as their slope.

In African rainforest species, the bulk of adaptive diversification takes place along the environmental gradient between rainforest and savanna. The differences in natural selection at different locations along that gradient produce inter-population variation in both phenotypic traits (e.g., shape and coloration) and genes that are important to survival and reproduction. Both evolutionary theory and empirical studies in other biomes indicate that the slope of an environmental gradient influences its potential to generate such adaptive variation. Typically, steeper gradients (indicating greater changes in environmental conditions) lead to more variation, and shallower (flatter) ones less.

Left: Adam Freedman working in the savanna-rainforest transition zone (known as the 'ecotone') in Cameroon. Right: Cows grazing at the edge of a gallery forest in the ecotone.

My dissertation research at UCLA included multiple field seasons during which I witnessed firsthand how deforestation was changing the vegetation structure of rainforest to something much more savanna-like. I wondered about whether such changes were extensive enough to cause the rainforest-savanna gradient to become shallower. In other words, had human-caused deforestation actually flattened the gradient and, as a result, led to a loss of variation in adaptive phenotypic traits along it? A satellite-derived tree cover map of Africa suggested a potentially valuable natural experiment. Despite ongoing deforestation, the rainforest-savanna gradient in Central Africa is still relatively intact. In contrast, deforestation has been so extensive in West Africa that many areas historically occupied by rainforest actually have less tree cover than the savanna. My hypothesis was that the inter-regional difference in deforestation should lead to greater phenotypic variation along the rainforest-savanna gradient in Central Africa than in West Africa.



Flattening of the rainforest-savanna gradient in West Africa.

To test this hypothesis, our team investigated the relationship between tree cover and morphological variation in the Little Greenbul (*Andropadus virens*), a species of songbird in the Pycnonotidae family that is found in more than 25 countries in Africa. *Andropadus virens* was an ideal test subject, as over the past two decades studies by CTR Director Tom Smith had confirmed the evolutionary significance of the rainforest-savanna gradient for this species. First, we quantified the slope of the tree cover gradient in both Central Africa and West Africa, using satellite imagery, and confirmed that it was far flatter in West Africa. Second, we established a quantitative relationship between tree cover and a number of adaptive morphological traits. Third, and consistent with our predictions, we determined that, for those traits, morphological divergence along the gradient was strong in Central Africa but absent in West Africa.

*Left and right: Little Greenbuls (*Andropadus virens*) from Cameroon, Central Africa.*

All of the above findings implicated human deforestation as the force driving loss of adaptive variation in West Africa. However, an important piece of information was missing. What did *Andropadus virens* look like historically, prior to the onset of extensive deforestation following World War II? To satisfy our curiosity about this, CTR Director Tom Smith and I traveled to the Natural History Museum at Tring, in the United Kingdom, which houses the largest collection of African birds from the 19th and early 20th centuries. With help from bird curator Dr. Mark Adams, we gingerly poured through trays of birds, trying not to ingest any of the arsenic preservative customarily used by colonial-era collectors. While we were able to find very few *Andropadus virens* from the rainforest-savanna transition zone (known as the 'ecotone'), we found that the *Andropadus virens* we examined from West and Central African rainforests were more similar prior to deforestation than they are today. Moreover, birds from the rainforest in West Africa, in response to deforestation, had become more like their counterparts inhabiting the ecotone.

This brings us back to the question, "Why care?" An overwhelming body of scientific evidence indicates that most adaptation to novel environments relies on standing genetic variation, that is, variation already existing within a species' gene pool. This is particularly true for relatively rapid environmental perturbations such as human-mediated climate change. If ecological gradients harbor much of the standing genetic variation we observe in the natural world, flattening them reduces it, constraining species' future potential to adapt to changing environmental conditions. In West Africa, deforestation had flattened the gradient, and a rapid evolutionary response in *Andropadus virens* had led to a loss of variation in morphological traits that are important for local adaptation.

We suspect that the reduction in adaptive diversity found in *Andropadus virens* in West Africa will occur elsewhere on the continent in the face of ongoing deforestation and climate change, and that a similar fate awaits many of the species whose distributions span the rainforest-savanna gradient. More importantly, given the extent of deforestation in tropical environments worldwide, we suspect that gradient flattening, with its potential to exacerbate biodiversity loss, may tragically become a global phenomenon.

This new issue in conservation begs for a solution, one that can complement rather than replace current strategies whose focus is protecting “hotspots” within areas of high species diversity. Facing an environmentally uncertain future, we would argue that the best conservation strategy should include a form of evolutionary bet-hedging, one that conserves standing variation within species so that at least some populations will pass through the adaptive bottleneck that surely awaits them in a transition to a warmer world. If the flattening of gradients worldwide is reducing species' standing genetic variation, doesn't it make sense to protect the ecological gradients that generate variation?

To read more on this study, click here to view the online article in *PLoS ONE*.

Photo and figure credits: Trevon Fuller, Adam Freedman, Ryan Harrigan, Alex Kirschel, and Tom Smith.