measurements of ^{14}C from high-elevation trees in the Austrian Alps are consistent with corresponding values from temperate sites in Japan[9], Germany[10] and more thermally constrained forests in the Swiss Alps[12]. All studies demonstrate the precision of tree-ring dating back to the year 775. No single volcanic eruption was strong enough to trigger summer cooling sufficient to cause trees to remain dormant throughout the growing season, thus forcing a dating error due to missing rings. This behaviour has now been observed for records from different tree species growing at temperate low-elevations[9,10] and near the upper treeline[12], which is evidence that the records are correctly dated. The finding is striking because there have been at least 14 eruptions that exceeded a Volcanic Explosivity Index (VEI) of five over the past 1,200 years.

Given our motivation for testing the so-called temperature threshold-response hypothesis[4], it should be noted that state-of-the-art palaeoclimatic models use volcanic-induced forcings derived from sulfate loadings in polar ice cores[13] to define the timing and duration of atmospheric cooling after eruptions. Our study subscribes to the mounting evidence for the precise dating of tree rings. Accepting this as fact, we are left with four plausible explanations to account for the reported discrepancy between simulated and reconstructed post-eruption temperatures[4,6]: (1) the use of ring width instead of maximum latewood density[14]; (2) estimates of volcanic forcing are too strong for some events[15,16]; (3) models are too sensitive to volcanic forcing[17,18]; (4) incorrectly dated ice cores[3,19].

High-resolution ^{10}Be measurements from ice cores are, however, expected to improve ice-core dating, as well as the detection and attribution of climate forcing signals among different palaeoclimatic archives[19]. Furthermore, it is indisputable that a more systematic dendrochronological assessment of ^{14}C measurements around the year 775, including various species from a wider range of ecological settings around the globe, would offer additional independent evidence for our argument. ❐

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Author contributions
U.B. designed the study with input from J.E., L.W., M.S. and W.T. D.G. and L.W. (K.N.) performed Isotopic (dendro) measurements. All authors contributed to discussion and writing.

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CORRESPONDENCE:

Priorities for conservation corridors

To the Editor — Jantz *et al.*[1] take advantage of new, high-resolution estimates of biomass and vegetation carbon storage (VCS) to map areas throughout the tropics that, if protected, could simultaneously connect existing protected areas while also retaining large carbon stores. This study highlights how the growing wealth of remotely-sensed data can be used to intelligently and purposely design protected areas. Given the recent emphasis on carbon sequestration in establishing and funding protected areas[2], it is understandable that the authors took a largely carbon-centric approach when identifying their proposed conservation corridors. We argue, however, that there are more important factors that should be considered when evaluating and prioritizing potential corridors.

The principle motivation for establishing corridors is not to protect VCS but to allow individuals and even entire species to move between otherwise disconnected habitats[3]. Corridors should ideally be set up to connect similar habitats and cross through habitats similar to those being connected. Jantz *et al.* did not consider the habitat type or the species composition of the areas that they were connecting. Likewise, they did not consider the type of habitats contained within the proposed corridors in relation to the connected protected areas. Instead, the authors proposed corridors that would contain the greatest possible density of carbon and the greatest possible diversity of mammal species. Following these guidelines, high-priority corridors could theoretically be placed through high-biomass, high-diversity areas to connect different low-biomass habitats with distinct species compositions (for example, a corridor of rainforest connecting a savannah park to a dry forest park). In several places, such as in the southeastern Amazon, Jantz *et al.* suggest corridors through areas that are already heavily-modified and under intense human cultivation.

When prioritizing potential corridors for conservation, it is also important to consider climate-driven species migrations. Climate-driven species migrations are different from the more traditional movements of individuals and species in that they are directional, with species migrating from climatically unsuitable areas to more suitable ones[4]. For example, warming in the tropics will drive species migrations from the lowlands to the colder highlands[5]. By combining species distribution models with general circulation models, it is possible to predict where species are now and where they will need to be in the future, thereby helping to guide where conservation corridors should be established[6].

Even accepting a carbon-centric viewpoint, Jantz *et al.* have probably overestimated the long-term VCS in their proposed corridors. By definition, habitat corridors are long and skinny (on average, the proposed corridors are 41–55 km long and 2–3 km wide) and thus a large fraction of the total corridor area will suffer from edge effects. These edge effects can include, for example, biomass/carbon collapse due to the increased mortality of large trees at distances of up to 100 metres from the forest edge[7] and increased susceptibility to fire at distances of up to several kilometres from the edge[8]. The habitat within corridors will inevitably degrade due to pervasive edge effects, causing VCS to decrease over time[9]. In contrast, protecting large, contiguous blocks of natural habitat will result in more stable carbon dynamics as a larger proportion of the protected areas will be core habitat[10]. To protect biodiversity in a changing world, we need an extensive network of large, well-connected protected areas. The corridors that allow for these connections should be designed with species movements, not carbon storage, as the priority. ❐

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Reply to 'Priorities for conservation corridors'

Jantz *et al.* reply — We appreciate the points made by Feeley and Rehm and we recognize that a network of well-connected protected areas could be extremely valuable for preserving biodiversity in the context of increasingly intense land use and climate change. It is clear that the increasing isolation of protected areas is exacting a toll on tropical species[1].

We agree that focusing on vegetation carbon stocks (VCS) alone cannot be expected to result in conservation corridors that are optimal for movement, migration and the dispersal of specific species. This was not, however, the primary objective of our research[2]. Instead, we focused primarily on investigating the potential for biodiversity co-benefits in the context of tropical emissions avoidance policies that consider not only deforestation and VCS, but also the contiguity of carbon stocks. Carbon finance is one of the most promising instruments for conserving existing forest habitat outside of parks and protected areas. Directing funds in a systematic manner, such as we describe via a network of corridors, could undoubtedly be a policy option for maintaining or even restoring continuous habitats while also preventing or mitigating habitat fragmentation — a process that threatens species viability, particularly under climate change.

The degradation of carbon stocks over time due to edge effects is a potential risk, and may happen in narrow corridors, but in many cases we expect the opposite to occur. Forests will regrow in degraded areas, on abandoned slash-and-burn agriculture landscapes and between existing forest fragments. All of these areas exist within our corridor network, and they offer the best solution for connecting protected areas. There is enormous potential to use these areas to our collective advantage, by allowing forests to regrow where they are most needed for biodiversity while sequestering atmospheric carbon in the process — another benefit of the corridor approach we propose. Moreover, allowing this process to occur in riparian forests, where many of our corridors are located, has the additional benefit of protecting water resources and associated aquatic biodiversity.

We also agree that connecting similar habitat types is preferable in most circumstances. This will typically be the case as we consider nearest-neighbour protected areas in a pairwise fashion. However, where the spatial turnover of habitat is high, homogenous corridors will not always be achievable. While species will disperse more readily through their preferred habitat, they may still disperse through similar intervening habitats, making corridors that traverse multiple habitats valuable for conservation. Indeed, a variety of corridor types will likely be necessary to maintain tropical biodiversity in the coming decades. Those that connect the same habitat types and those that connect habitats across environmental gradients can both facilitate species movement under climate change while also avoiding deforestation and forest degradation outside of protected areas.

There are many applications for these corridors and many ways that they can be improved and considered for use in various management contexts. To that end, we have made the data freely accessible (www.whrc.org/corridors).

We encourage the exploration and assessment of corridor utility in the context of national, regional and local land-use priorities and forest conservation activities, as well as in the broader context of REDD+ implementation. We also welcome feedback on their utility for these applications and on the ways that they can be improved. ❐

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