alone. Restrictions imposed by specific fabrication processes, whether technological or biological, can be an important factor in shaping a mechanical structure. Such restrictions were not included in Aage and colleagues' study. The architectures of natural materials are also known for their remarkable fracture toughness[7] (a measure of resistance to crack propagation), but this is not yet a commonly used criterion in computational design. Another future challenge will be to enhance the authors' high-resolution framework with capabilities to handle design problems involving, for example, time-dependent behaviour, which requires additional computational effort.

The design of Aage and colleagues' aircraft wing involved 8,000 computer processors used over several days. Few people will have access to such resources in the foreseeable future. Therefore, to enable a wider community to reap the benefits of the authors' work, it is imperative to find ways to more efficiently produce high-resolution designs. For example, the fact that very small structures were seen only in specific areas of the designed wing could allow for adaptive adjustment of resolution, which would reduce computational cost. Nevertheless, the authors' work represents a leap forward in the capabilities of computational design. Without doubt, its unprecedented resolution provides the foundation for further discoveries. ■

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ECOLOGY

A matter of time for tropical diversity

There is a species-diversity gradient on Earth, with the greatest diversity found near the Equator. Analysis of forest data now reveals a mechanism aiding species coexistence in the tropics that might underlie this phenomenon. **SEE LETTER P.105**

GARY G. MITTELBACH

The tropics teem with a diversity of life that is much richer than elsewhere on the planet. For example, there are 1,175 tree species in half a square kilometre of forest in Borneo, a greater number than the estimated 1,166 tree species in all the temperate forests of Europe, North America and Asia combined[1]. The striking increase in species number moving from the poles to the Equator, known as the latitudinal diversity gradient, is Earth's most striking biodiversity pattern. Yet its underlying causes have mystified biologists for more than a century, leading the ecologist Robert Ricklefs to famously state[2] that this pattern "mocks our ignorance". Usinowicz *et al.*[3] reveal on page 105 how an ecological theory[4,5] that models species coexistence might illuminate the latitudinal diversity gradient of trees.

Understanding this diversity phenomenon requires a grasp of processes that generate biodiversity on large spatial scales, including speciation, extinction and migration, as well as processes that allow multiple species to coexist within a community. Various evolutionary processes might promote higher rates of speciation or lower rates of extinction in tropical rather than temperate environments[6], thereby generating greater regional diversity in the tropics over evolutionary time. But how is this diversity maintained locally within a given forest? Usinowicz and colleagues show that species coexistence is promoted in tropical forests because species there have greater negative effects (through processes such as competition) on members of their own species than they do on members of other species.

> ***"The coexistence of tree species may be enhanced at lower latitudes because of stronger intraspecific competition at the seedling stage."***

Usinowicz *et al.* assembled a multi-year data set of annual seed production and seedling survival (an estimate of the annual 'recruitment' to a species' population) for well-sampled tree species in ten forests distributed from near the Equator to a latitude of 65° N in Alaska.

50 Years Ago

The British preoccupation with the need to persuade young people into science and engineering, but particularly the latter, was continued last week by the Research and Development Society … Adults, at least, are prepared to take the subject seriously … the British educational system is designed to produce "cultured gentlemen", with the result that trained scientists consider that collaboration is a kind of cheating, that engineering is inferior and that the profit motive is even worse. Yet teamwork, technology and business sense are essential for the survival of the British economy. But what if you cannot even bring the horse to the water, let alone persuade him to drink properly? … One of these days something may be done about it.
From *Nature* 7 October 1967

100 Years Ago

I have spent a good many hours lately in a Devonshire garden in which there was a border of massed mauve asters which was a great attraction to butterflies … The object of my letter is to describe to your readers two "scraps" which I witnessed between tortoiseshell butterflies and wasps, in each of which the butterfly was victorious … The butterfly sprang on to the back of the wasp, the head of each being towards the tail of the other, and a furious rough-and-tumble took place some 6 ft. from the ground. The wasp was unable to use its sting, as the butterfly was on its back, and at the end of perhaps five seconds the butterfly, which had been buffeting the wasp with its wings, dropped to within a foot of the grass, relaxed the hold which it had exerted, and allowed its enemy to drop breathless and beaten on to the lawn. Nature had taught the butterfly to adopt the same tactics … which enabled G. Carpentier to win his fight with Bombardier Wells.
From *Nature* 4 October 1917

They found that the synchrony of the timing of seedling recruitment between different tree species was less in forests near the Equator than in forests closer to the pole (Fig. 1). Northern trees have a shorter growing season than trees in tropical forests. This latitudinal difference in growing-season length enables tropical tree species to differ more in their timing of seed production and seedling recruitment compared with species that grow in temperate or boreal conditions.

Why might this promote species coexistence in the tropics? According to ecological theory[4], any factor that causes a species to compete more strongly with individuals of its own species than with individuals of other species will favour species coexistence, because a species will limit its own population growth more than it limits the population growth of other species.

Asynchrony in the timing of seed production between forest trees could affect the strength of within-species versus between-species seedling competition and survival as follows. In forests in which the growing season is short, every species must produce and disperse its seeds at around the same time, so seedlings will compete with the seedlings of many other species for light and nutrients. However, if the growing season is long and species produce and disperse their seeds at different times, then the competitive interactions between seedlings will be concentrated among individuals of the same species. Moreover, if there is pronounced year-to-year variation in seed production, years of high seed production will lead to greater within-species seedling competition in asynchronously reproducing species than in more-synchronously reproducing species.

This coupling of 'good' years for reproduction with more-intense intraspecific competition is a key component of species-coexistence theory, and is known as the storage effect[4,5]. The name comes from another important aspect of the effect: the positive influence of good years of recruitment that boost population growth is 'stored' in a long-lived life stage (adult trees, in this case), allowing the population to withstand the negative effects of years in which recruitment is poor.

To test whether the variation in recruitment timing observed in the ten forests is sufficient to increase the probability of species coexistence at low latitudes, Usinowicz and colleagues incorporated species-recruitment data into a mathematical model of forest dynamics that was similar in form to the original storage-effect model[5]. They found that the relative strength of interspecific-to-intraspecific competition in forest trees decreased by 0.25% for each degree of latitude closer to the Equator, and that latitudinal variation in climate underlies this effect. Thus, the coexistence of tree species may be enhanced at lower latitudes because of stronger intraspecific competition at the seedling stage.

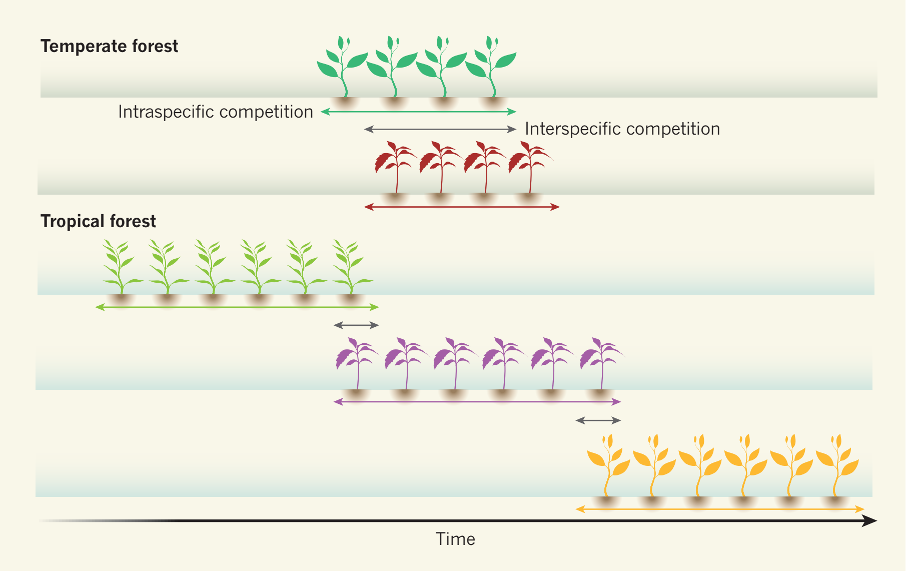

Figure 1 | Seedling growth in temperate and tropical forests. Usinowicz *et al.*[3] investigated factors that might be responsible for the greater diversity of tree species observed in tropical forests near the Equator compared with that in temperate forests at higher latitudes, by analysing seed and seedling data from ten forests at different latitudes. In temperate forests, there is a short growing season and a lot of overlap in the timing of seed production and growth of seedlings from different species (shown in different colours). This leads to a high level of intraspecific and interspecific competition, because species experience similar environments. However, the growing season is longer in the tropics, and the authors found that there is less overlap in the timing of seed production and seedling growth of different species. This allows species in the tropics to experience environmental conditions differently, increasing the relative strength of intraspecific competition compared with interspecific competition. High levels of intraspecific competition can help to promote species coexistence and therefore boost species diversity[4].

The findings made by Usinowicz and colleagues are especially exciting, given that another recent study of forest trees[7] also found pronounced latitudinal variation in the strength of intraspecific versus interspecific interactions, which occurred through a different ecological mechanism. The authors of that study[7] of 24 forest plots worldwide found that the growth and survival of individual forest saplings were more strongly negatively affected by the density of neighbouring trees of the same species than by that of trees of a different species. Moreover, this negative density-dependence phenomenon[8,9] was stronger for rare species in tropical forests than for those in temperate forests, a factor that should also promote species coexistence in the tropics. The work by Usinowicz and colleagues and this other study[7] provide complementary evidence that the high diversity of tropical trees may be facilitated by ecological mechanisms that result in tropical-forest species more strongly limiting their own species compared with the intraspecific self-limitation that occurs in temperate and boreal forest species.

Usinowicz *et al.* found a linear relationship between latitude and the relative strength of intraspecific-to-interspecific competition, with greater competition closer to the Equator. However, the number and geographical distribution of the studies from which they assembled data for analysis are less than ideal. There are no sites in Africa, Europe or Central Asia, and five of the ten forests are on islands. Also, one might expect the relationship between latitude and synchrony in recruitment (and the relative strength of intraspecific competition) to be nonlinear, changing more sharply at the northern and southern boundaries of the tropics (at approximately 23° latitude from the Equator). Additional long-term studies of recruitment dynamics in forests across the globe are needed to resolve these points, along with studies examining how the strength of the storage effect varies with latitude in other organisms. But that work is for another day, and now is the time for ecologists to delight in evidence showing a link between fundamental mechanisms of species coexistence and broad-scale patterns in climate and biodiversity. ■

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This article was published online on 20 September 2017.