ECOLOGY

Lasting signature of forest fragmentation

Animal communities that endured historical environmental upheavals are less sensitive to modern ones

By Anna Hargreaves

A universal truth of ecology is that field experiments never unanimously support theory. This is not (always) because ecological theory is poorly developed or experiments poorly executed, but because ecology is a complex science dealing with variation at every biological level from individuals to biomes. When exceptions are the rule, explaining variation in responses among taxa and locations becomes the goal, particularly for theory that informs conservation. On page 1236 of this issue, Betts et al. (1) contribute to a particularly important debate: why the biological effects of forest fragmentation are so variable among species and places. They present evidence that historical deforestation (from glaciation, fires, hurricanes, or anthropogenic clearing) yielded communities that are more robust to modern forest fragmentation (from logging, burning, or development).

Humans are rapidly converting natural habitats (2), and the effects come in two flavors: loss and fragmentation. The negative impact of habitat loss is undeniable: Populations decline; species go locally extinct. Indeed, after direct exploitation, habitat loss is the primary cause of past extinctions (3) and a serious threat to modern biodiversity (4). Fragmentation refers to the spatial arrangement of the remaining habitat after some is lost, in particular the frequency of habitat edges. The relative impact of fragmentation after accounting for habitat loss has been the subject of raging debate since the early 2000s (5–8). Whereas landscape-level tests are still too rare to reach robust conclusions, case studies show that fragmentation per se can be devastating for some taxa in some places but surprisingly positive for others (9). This variation has not yet been convincingly explained.

Although the ecological effects of fragmentation have been studied extensively (if not conclusively), the evolutionary implications have not. Short-term evolution after fragmentation has been documented, albeit rarely, mostly involving changes in dispersal or mating systems (10). Such evolution could help populations survive in fragmented landscapes (for example, evolution of increased dispersal ability could reduce perceived fragmentation) but could also create evolutionary traps (for example, evolution of decreased dispersal might doom populations to stay in disappearing patches) (11). The jury is out on whether evolution will be rapid enough and in the right direction to help species cope with modern fragmentation. Even less is known about the long-term evolutionary effects of historical fragmentation.

Betts et al. tackle these gaps through the lens of extinction filters. The extinction filter hypothesis proposes that historical exposure to a stressor filters a community to species that can cope with that particular stressor (12). This hypothesis has most famously been applied to ancient human hunting, proposing that areas with a longer history of human exploitation have faunas that are less vulnerable to modern exploitation (13). Extinction filters can operate evolutionarily if species adapt to tolerate the disturbance, or ecologically if sensitive species are lost during disturbance. Betts et al. predict that animal communities in forests historically prone to edge-creating disturbances should be more resilient to modern fragmentation, either because species have adapted to edge effects or because sensitive species have already been purged. Consistent with the extinction filter hypothesis, Betts et al. find fewer species that specialize on interior forest habitat and less edge avoidance in forests with a history of severe disturbance in the past 10,000 years.

These results partly rest on correctly identifying areas with historical edge-creating disturbances. The authors define such areas as those subject to regular hurricanes, forest fires, or glaciation (all binary variables), or recent human deforestation measured as the amount of intact forest predicted to exist by 2000. The time scale of these disturbances is clearly highly variable, and their primary effect is undoubtedly forest loss. But because even glaciers have uneven edges and storms leave pockets untouched, it is reasonable to assume that these events created increased edge effects and some degree of fragmentation as well.

Taken together, these disturbances leave a band of low-disturbance forest concentrated around the equator. Accordingly, Betts et al. found that tropical forest communities are more sensitive to edge effects, and that the proportion of forest-core specialists in-
creases from high to low latitudes, contrary to results of a recent review that found no difference in sensitivity between tropical and temperate taxa (9).

Support for the extinction filter hypothesis can be interpreted optimistically or pessimistically for conservation, depending on whether filtering is evolutionary or ecological. If historically disturbed communities can successfully adapt to disturbance, we might hope that future evolution will rescue at least some of the habitat specialists currently threatened by fragmentation. Betts et al. found that past human deforestation—arguably the disturbance with the shortest evolutionary time scale—was a much weaker predictor of edge sensitivity than natural disturbances. Perhaps evolution simply has not had time to mitigate the ill effects of human activity.

However, the measure of historical human deforestation used by Betts et al. only includes areas that were still deforested as of 2000. The true extent of human forest use in the past 10,000 years is controversial, particularly in the Americas, where European contact in 1492 wiped out 90% of indigenous inhabitants (numbering in the millions) in as little as a generation (14). Recent estimates suggest this “great dying” led to the reverting of cleared areas to forest (15). If species could evolve to cope with human forest fragmentation on evolutionary time scales (extinction filtering via adaptation), we might expect modern deforestation to overpredict sensitivity in areas where forests regrew before 2000. In fact, Latin American forests make up most of the low-disturbance communities in the analysis and seem disproportionately sensitive to fragmentation. If extinction filtering results instead from purging of sensitive species, Betts et al.’s results suggest a grim future for tropical forest specialists that are rapidly running out of intact forest in which to seek refuge (2).

REFERENCES AND NOTES

IMMUNOTHERAPY

Ushering along B cells to neutralize HIV

Progress in staged immunizations designed to elicit a vaccine response is reported

By Amanda Agazio and Raul M. Torres

Although vaccines are a great achievement in medicine, HIV, with its extraordinary dynamic diversity, is not restrained by classic vaccine approaches. In 2009, after the RV144 vaccine trial results revealed suboptimal HIV protection, effort focused on developing vaccines able to elicit antibodies that can protect against a breadth of HIV genetic variants. Ten years on, such HIV broadly neutralizing antibodies (bnAbs) are known to display unusual features compared with typical antibodies. These features almost certainly impede eliciting bnAb generation with a vaccine. On pages 1215 and 1216 of this issue, Saunders et al. (1) and Steichen et al. (2), respectively, use custom-designed HIV envelope (Env) proteins as immunogens to promote unusual antibody features needed for neutralization and to recruit rare bnAb-precursor B cells into antibody responses. These studies demonstrate progress in eliciting antibodies with the potential to provide a breadth of HIV neutralizing activity.

In the past decade, numerous technological advances have greatly facilitated the identification and characterization of bnAbs from HIV-infected individuals. These include single cell–based approaches to identify HIV-specific B cells, molecularly clone their antibody receptors, and rapidly screen for specificity and neutralizing activity. When coupled with bnAb-Env structural analyses, the development of stable Env proteins and computational design have led to custom-designed Env proteins that are able to recruit rare B cells into an antibody response and have fueled progress toward an HIV vaccine (3, 4). Many hundreds of bnAbs have now been isolated from HIV-infected individuals and characterized to reveal that bnAbs recognize one of a few conserved regions, or epitopes, on Env and neutralize by preventing HIV association with the CD4 T cell receptor (the target of infection) and blocking virion-cell fusion.

Critically, bnAb recognition of these neutralizing epitopes requires one or more unusual features not normally observed in antibodies elicited by other pathogens. For example, the immunoglobulin (Ig) heavy chain region that contacts Env [heavy chain complimentary-determining region 3 (HCDR3)] is often much longer in bnAbs compared with other antibodies. In the course of a normal antibody response, Ig genes are mutated to increase antibody affinity for the targeted pathogen (affinity maturation), and bnAbs are also unusual in that they display a high frequency of mutations, including rare mutations that are difficult to generate but important for broad recognition of HIV variants. Longitudinal studies of HIV-infected individuals have characterized the coevolution of Env and antibody responses to reconstruct the trajectory, or lineage, of a bnAb from the original unmutated antibody, highlighting the mutations that are important for neutralization (5).

Together, these studies motivated an Env structure–based approach in which distinct engineered immunogens, through sequential immunizations, drive the maturation of Env-recognizing B cells to produce bnAbs. An initial immunogen would elicit (and numerically expand) naïve B cells expressing unmutated antibodies into an antibody response with the potential to further develop into a bnAb. Immunization with a second immunogen would select responding B cells with specific antibody mutations that are important for recognition of the neutralizing epitope (see the figure). In this manner, serial immunizations would usher B cells with specific somatic mutations to ultimately generate a B cell population that secretes antibodies capable of providing a wide breadth of neutralizing activity against HIV (1, 6, 7). Previous studies using mice with B cells engineered to express bnAbs (4, 8) demonstrated feasibility and provided an impetus for pursuing this approach.

A major issue addressed by Saunders et al. is that bnAbs often require mutations for neutralizing activity that are not typically introduced into antibodies during the
Lasting signature of forest fragmentation
Anna Hargreaves

*Science* 366 (6470), 1196-1197.
DOI: 10.1126/science.aba1103