

Churlish though it might seem to muddy the elegant simplicity of the Robertson–Price/Lande–Arnold approach for describing selection, these recent studies underline the need for more caution in describing the forces of natural selection. They provide strong evidence that environmental covariances can bias our estimates of selection; in doing so, the results highlight the benefits to be gained by considering genetic, rather than simply phenotypic, measures when trying to understand the evolution of quantitative traits. They also provide a potential explanation for the widespread lack of correspondence between predicted and observed evolutionary trajectories in natural populations [12].

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Slow burn: the insidious effects of surface fires on tropical forests

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Accidental surface fires are emerging as one of the most pervasive threats to tropical forests. Although unimpressive in appearance, these fires can have surprisingly potent impacts on rainforest plant and animal communities, as demonstrated by recent studies led by Jos Barlow and Carlos Peres in central Amazonia. Even worse, surface fires greatly increase the likelihood of far larger conflagrations that can lead to complete forest destruction.

Each year, thousands of fires are lit in the humid tropics, to raze vast expanses of forest for ranching and slash-and-burn farming. Although highly destructive to natural ecosystems, these intentional fires are now being rivaled in terms of their ecological impacts by a more subtle menace: accidental surface fires.

Surface fires are deceptively unimpressive, creeping along the forest floor as a thin ribbon of flames and rarely exceeding 20 cm in height (Fig. 1). Unlike fast-burning intentional fires, which are lit after vegetation has been slashed and felled to dry out forests and increase flammability, surface fires merely consume the leaf and woody litter and generate only modest heat, covering as little as 150 m in a day [1].

Nevertheless, surface fires are deadly to many rainforest plants, which typically have thin (< 1-cm thick) bark and thus are highly vulnerable to heat stress [2,3]. Studies conducted 1–2 years after a surface fire suggest that the



Fig. 1. A surface fire creeping through the rainforest understorey in eastern Amazonia. Reproduced with permission from Mark A. Cochrane.

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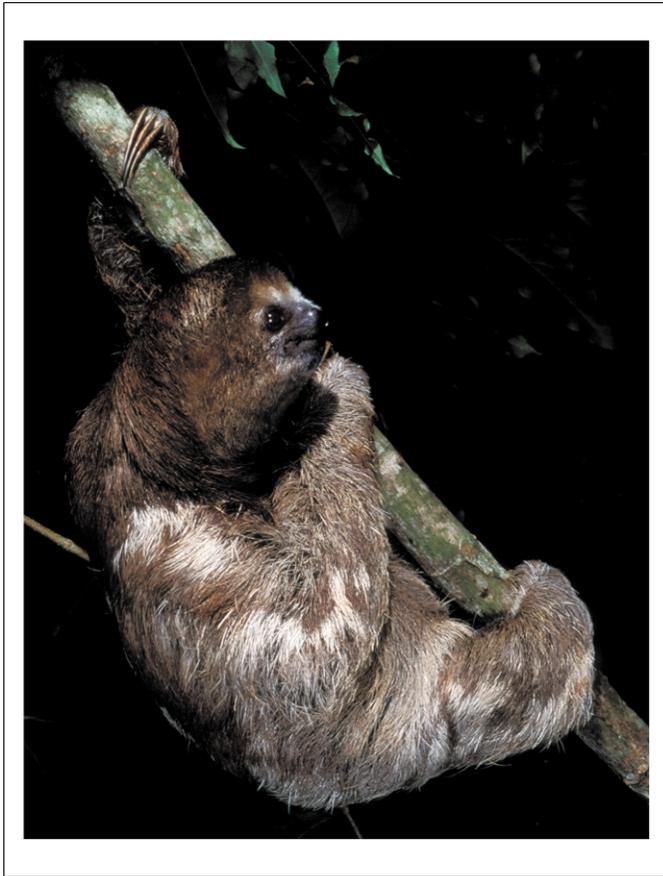


Fig. 2. Slow-moving animals, such as three-toed sloths *Bradypus variegatus*, suffer heavy mortality during surface fires. Reproduced with permission from Andrew M. Dennis.

slow-moving flames can girdle and kill a third or more of all trees (at least 10 cm in diameter) and most vines and ground forbs [1,4–6]. Saplings and small trees, which have proportionally thinner bark compared with large trees, are especially vulnerable [1,2,4].

Impacts on rainforest biotas

Several recent or forthcoming studies, led by Jos Barlow [3,6–8] and Carlos Peres [9] from the University of East Anglia, UK, now reveal that surface fires can have profound impacts on Amazonian wildlife. The fire that they studied, in a relatively seasonal area of the central-eastern Amazon, degraded at least 1100 km² of forest during the strong El Niño drought of 1997–1998. The burn apparently arose from a single source, probably as an escaped agricultural fire lit by local villagers.

The immediate effects of the fire were striking. Numerous animals, including monkeys, marmosets, sloths, peccaries, deer, parrots, toucans, snakes and lizards, were killed or injured. Most vulnerable were species with low mobility (Fig. 2), poor climbing ability, or a reliance on cavity nests in trees [9]. Villagers reported sharp declines of army ants, understory wasp colonies and leaf-litter invertebrates, such as spiders and centipedes. Burnt forests were remarkably silent, even at dawn and dusk when the vocal activity of birds and monkeys peak, suggesting that even mid-story and canopy species had been killed or driven away by smoke asphyxiation, or had fled when maturing fruit crops in

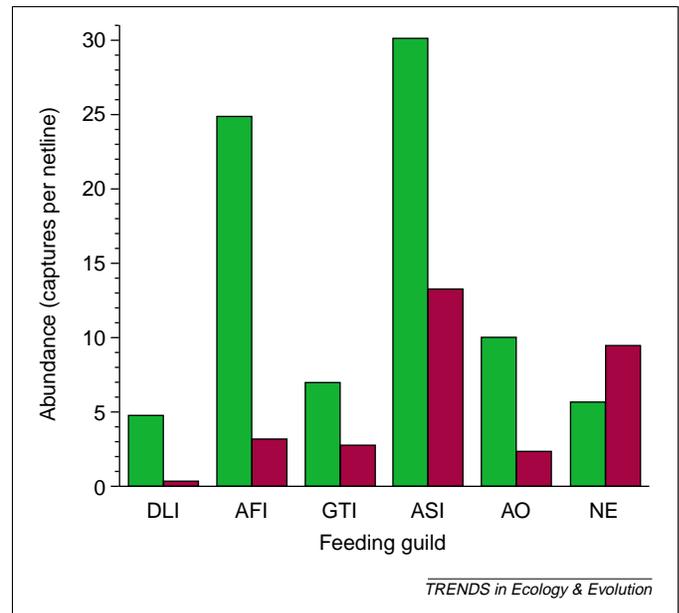


Fig. 3. Dramatic disruption of foraging guilds of understory birds in recently burnt Amazonian forests (unburnt forests, green bars; burnt forests, red bars). Abbreviations: AFI, army ant-following insectivores; AO, arboreal omnivores; ASI, arboreal sallying insectivores; DLI, dead-leaf-foraging insectivores; GTI, gleaning terrestrial insectivores; NE, nectivores. Adapted from [7].

damaged trees were aborted. The initial declines of wildlife were exacerbated by local hunters, who killed many stressed or injured animals [9].

By 10–15 months after the fire, an average of 36% of all trees, three-quarters of all saplings, and many lianas had died. Canopy openness was four times greater than in unburnt forest (ranging from 12–32%) and light levels had risen dramatically in the forest understory [6,9]. As a result, a dense flush of vegetation, dominated by disturbance-loving pioneer trees, bamboo, sedges and coarse herbs, had proliferated in the understory. Moreover, tree and liana species bearing fleshy fruits, which provide key food resources for wildlife, had much higher mortality than did species with inedible hard or wind-dispersed seeds [9].

Such dramatic changes in forest structure, microclimate and resource availability had especially strong effects on bird communities [7]. Mist-net samples collected one year after the fire revealed that understory birds were much less abundant in burnt than in unburnt forest, and the trophic structure of bird communities was profoundly altered (Fig. 3). Specialized insectivores, such as army ant-followers (Fig. 4), dead-leaf gleaners, terrestrial gleaners, and arboreal sallying insectivores were most severely affected, whereas nectar- and seed-eating species increased sharply. The birds most harmed by the fire were uncommon, disturbance-sensitive and habitat specialists – the same species that are highly vulnerable to habitat fragmentation and logging [7–9].

Yet more changes in the fauna of burnt forest were evident. Terrestrial browsers and foragers, such as deer, large rodents, armadillos and forest tortoises, increased in abundance in response to dense foliage and cover in the understory. Other species that favour secondary forests also increased, sometimes dramatically.



Fig. 4. Foraging specialists, such as this scaled-backed antbird *Hylophylax poecilonota*, decline precipitously in burnt forest. Reproduced with permission from Andrew M. Dennis.

Returning three years after the fire, the researchers made some remarkable observations. Many additional trees had died, especially larger trees (≥ 50 cm diameter), from fire-induced injuries. As a result, total tree mortality rose to 48% after the fire (compared to just 4% in unburnt forest), and nearly half (49%) of the living tree and liana biomass was killed [6]. If these delayed effects are typical, then surface fires could have much greater impacts on forest ecosystems than was previously thought. Moreover, the collapse of biomass in lightly burnt forests might be a globally important source of greenhouse gas emissions. The authors estimate that, during strong drought years, surface fires in Brazilian Amazonia might produce carbon emissions that are equivalent to 10–12% of that generated by the worldwide burning of fossil fuels [6,8].

The surface fires also affected several local villages, destroying nearly all cassava plots and many fruit trees, perennial crops and natural fibers used for weaving and house construction. To compensate for their losses, the villagers began hunting intensively, further increasing impacts on wildlife. More than a third of all medium- to large-sized vertebrates (13 out of 35 species) were extirpated from burnt areas, including sensitive species, such as tapir *Tapirus terrestris*, white-lipped peccary *Tayassu pecari*, white-fronted capuchin monkey *Cebus albifrons* and giant armadillo *Priodontes maximus*. Furthermore, by decreasing the quality of life for villagers, the fire aggravated pressure for frontier expansion into remote upstream areas [9], potentially increasing deforestation in the region.

Escalating surface fires

Two decades ago, tropical wildfires were not a serious conservation issue, but today they are considered one of the most critical threats to tropical forests [4,5,10–15]. One key reason is that, once initially burned (even by a light surface fire) rainforests become vastly more prone to successive and ever more-intensive fires (Box 1). The extreme vulnerability of rainforest plants and animals occurs because fire is largely foreign to these ecosystems (although fire incursions have occurred rarely in the past

Box 1. In rainforests, fire begets fire

Even more alarming than their initial impacts is that surface fires can set in motion an irreversible process of forest degradation. The initial fire in rainforests typically kills 10–40% of all trees and most vines [1,4,13]. As a result, the forest canopy becomes fragmented and the quantity of dead fuels increases as dead leaves and trees begin to fall. Soon, the forest is vastly more prone to subsequent fires, because the diminished canopy enables rapid drying to occur and the dying vegetation provides large quantities of combustible fuel.

The second fire is far hotter and more destructive than the initial burn, killing 40–50% of remaining trees [1,4] and overwhelming even large, thick-barked trees [26]. Moreover, whereas the initial surface fire might require an extensive drought, subsequent conflagrations can occur after just a few weeks without rain [4].

During the first several fires, more fuels are created than destroyed, and a positive feedback results in which each fire becomes more likely and intensive. This process can eradicate rainforest trees and promote extensive grass invasion, converting rainforests into anthropogenic savanna or degraded scrub. In regions with strong dry seasons, this degradation process can be almost irreversible once it is initiated [1].

millennia [16–18]), except in drier, marginal areas where species are somewhat more resilient to fire [2,3].

Today, surface fires are growing alarmingly in importance, for three reasons. First, prevailing land uses in the tropics, such as logging [5,10,12,19] and habitat fragmentation [14,20], greatly increase the vulnerability of forests to fire. Second, the number of ignition sources has risen dramatically as increasing numbers of slash-and-burn farmers and ranchers penetrate ever deeper into remote frontier areas; in the Amazon basin, for example, tens of thousands of individual fires are lit each year [21]. Finally, El Niño droughts are becoming more frequent and severe [22,23], possibly as a result of increasing greenhouse-gas concentrations [24,25]. During harsh droughts, even fully intact, unlogged forests can become vulnerable to surface fires [5,9,15].

Unfortunately, it is still very difficult to determine the true extent of surface fires in dense tropical forests, because prevalent satellite-monitoring methods (e.g. Advanced Very High Resolution Radiometer or Landsat Thematic Mapper) are generally ineffective at detecting scorched forest understories. However, new high-resolution satellites and specialized detection algorithms are becoming available [15], and could prove more useful for the key task of mapping fire occurrence. Equally vital is the need to better understand the ecological impacts of wildfires throughout the tropical biome, with its great diversity of forest types and land-use practices, and to predict the effects of regional and global climate change on fire incidence. For, as studies such as those of Barlow and Peres reveal, even low-intensity fires can have surprisingly destructive effects on rainforests and their biotas.

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Environmental autocorrelation: curse or blessing?

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Theory of population dynamics predicts that environmental autocorrelation increases extinction risk. Recent work by Engen and colleagues confirms this and demonstrates how the spatial extent of population synchrony is influenced by dispersal. However, in a new study, Gonzalez and Holt demonstrate that environmental autocorrelation causes substantial increases in the size of populations with negative growth rates, provided that they are sustained by immigrating dispersers. These new findings could change our view of dispersal and sink populations, whilst providing an explanation for previously enigmatic population outbreaks.

Environmental variability influences population dynamics in many ways. Over the past two decades, much attention has been paid to spatial and temporal correlations among environmental features, because correlated environments can cause populations to fluctuate synchronously (the 'Moran effect' [1]), which increases extinction risk [2–5]. Environmental correlation is defined as the covariance of environmental parameters in space or time and I use this neutral term here when the source of the correlation (i.e. spatial or temporal) is not relevant for the effects being discussed. Spatial autocorrelation (e.g. a storm affecting an entire region) could prevent the successful recovery of locally extinct or critically declined populations,

because the distance to the nearest unaffected population might be too great for potential immigrants to overcome. Depending on the degree of isolation, temporal autocorrelation (e.g. a series of bad years) might also decrease population sizes such that the species disappears from a given locality. The spatial scale at which environmental correlation occurs critically influences extinction risk, because large-scale events have a greater impact than do small-scale events. However, a recent study by Gonzalez and Holt [6] sheds new light on the role of environmental correlation in population dynamics. The authors provide both theoretical and empirical evidence that environmental correlation can inflate the sizes of populations with negative growth rates, and even lead to population outbreaks. These findings could revolutionize our view of environmental autocorrelation and declining populations.

Environmental autocorrelation leads to inflated sizes of sink populations

Gonzalez and Holt [6] used a system of spatially separated populations in which some populations, so-called 'sink populations', could persist only because of immigration from 'source populations' [7,8]. Evidence for source-sink dynamics comes from several empirical studies [9,10]. Gonzalez and Holt [6] showed mathematically that, in constant environments, the equilibrium size of populations with negative growth rates equalled the immigration: absolute value of growth rate ratio. Hence, the equilibrium

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