Edge effects and ecological processes: are they on the same scale?

'Do edge effects occur over large spatial scales?' In his recent *TREE* News & Comment article, Laurance posed this insightful question and then answered it in the affirmative for three recent case studies – bearded pigs, wild pigs and large carnivores[1]. However, the interaction he described for wild pigs and an exotic shrub in Peninsular Malaysia might be incorrect. He correctly attributes the high density of pigs in the Pasoh Forest Reserve to abundant food in the adjacent matrix – a sea of African oil palms whose fruits are devoured by pigs. However, he neglects to mention another essential factor for high population densities – a lack of predators. Tigers and leopards have been eliminated from the reserve, many being shot after straying onto adjacent plantations, thus confirming the Woodroffe and Ginsberg[2] prediction. Based on our 1996 and 1998 estimates, wild pigs at Pasoh maintain a hyperdense population in both mast and nonmast years, 10–100 times more dense than other populations that still harbour large predators.

Nonetheless, evidence connecting the presence of the exotic shrub *Clidemia hirta* with elevated pig densities at Pasoh is purely circumstantial. Furthermore, this bird-dispersed species has invaded numerous tropical locations worldwide, many outside the range of wild pigs. For example, *C. hirta* occurs within another aseasonal dipterocarp forest of Southeast Asia, Sepilok Forest Reserve in Northern Borneo, where even the related bearded pig is rare. Consequently, the link between *C. hirta* and pigs remains tenuous, thus adding little support for Laurance's contention of large-scale edge effects.

However, there is a striking effect of the elevated pig densities at Pasoh, which supports Laurance's hypothesis: pigs remove understory saplings to build nests in which to give birth. Around each nest up to 500 saplings of less than 2.5 cm dbh (diameter at breast height) are removed, thus affecting stem density, light levels and diversity. Although localized intense perturbations at low frequencies might be a part of tropical forest dynamics, at such high frequencies (over a thousand nests annually throughout the 2600-ha reserve) these perturbations disrupt natural recruitment.

How is it that the large-scale edge effects characterized by Laurance have been overlooked in forest fragmentation studies? Perhaps ecologists have focused more on edges than on interactions between the matrix surrounding fragments and fragments themselves. When considering the matrix, we might expect the degree to which conditions have been altered to determine both the magnitude and the spatial scale of an edge effect, perhaps even causing fragments to collapse[3]. However, there might be another missing element in the analysis – namely, the scale of the ecological process affected by the edge. Simply put, the scale of an edge effect might be determined not just by conditions in the matrix but also, and perhaps more importantly, by the scale of the ecological process that is affected. At Pasoh, pigs roam 2–3 km to reach oil palms, thus the edge effect permeates the entire reserve. At a grander scale, bearded pigs in Borneo migrate 10–100 km to exploit mast[4].

If science is to heed Laurance's admonition of large-scale edge effects, we must also focus our attention on ecological processes that operate over large spatial scales.

Kalan Ickes

Dept of Plant and Soil Science, University of Aberdeen, Aberdeen, UK AB24 3UU
(kalan42@hotmail.com)

G. Bruce Williamson

Dept of Biological Sciences, Louisiana State University, Baton Rouge, LA 70803, USA
(btwill@lsu.edu)

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Reply from W.F. Laurance

Ickes and Williamson[1] make some interesting points and I accept their conclusion that the extirpation of large predators, in addition to an artificially increased food supply, has contributed to the hyperabundance of pigs at Pasoh Forest Reserve in Malaysia. The work supporting their conclusion is not yet published and I had based my interpretation on the forthcoming paper by Peters[2], who did not suggest the absence of large predators as a potential cause of increased pig numbers. As I emphasized in my original article, the extirpation of large predators in isolated nature reserves, such as Pasoh, could certainly have important ecological effects[3,4].

However, I do not agree with Ickes and Williamson's suggestion that the evidence linking elevated pig disturbances with the proliferation of *Clidemia hirta* at Pasoh is 'purely circumstantial'. Peters[2] showed quite clearly that *Clidemia* was mainly associated with sites having past soil disturbance, as well as treefall gaps, which had evidently been disturbed by pig rooting. In this sense, pigs definitely appear to be facilitating the germination and establishment of this tropical weed. In addition, Ickes and Williamson are overly simplistic in attributing the collapse of canopy–tree recruitment in Indonesia's Gulung Palung National Park solely to an influx of bearded pigs. Many other species – various primates, rodents, birds and insects – are also nomadic seed predators and probably contributed to the dramatic reduction in canopy–tree recruitment[5,6].

Aside from these details however, Ickes and Williamson and I are in complete agreement: edge effects may be occurring over far larger spatial scales than has previously been appreciated. Their suggestion that large-scale ecological processes might be particularly prone to far-reaching edge effects is an insightful hypothesis and could help focus future research efforts. I also agree with their proposition that the nature of the surrounding modified matrix can strongly influence edge effects and fragment dynamics – a conclusion supported by recent studies[7]. Indeed, I propose that we broaden the definition of 'edge effect' to include not only those phenomena in the immediate vicinity of forest edges but also the broader array of fragment–matrix interactions, at least insofar as these changes penetrate into fragments and disrupt natural processes.

I believe that many 'fragmentologists', myself included at times, have been somewhat myopic in their thinking about edge effects. This has caused them to focus on small-scale phenomena that are obvious and easy to study, while potentially missing the bigger picture. I have little doubt that we will find more large-scale edge effects once we start to look for them. The key goal now is to study these phenomena, and to try to determine their ubiquity and importance.

William F. Laurance

Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama; and Biological Dynamics of Forest Fragments Project, National Institute for Amazonian Research (INPA), CP 478, Manaus, AM 69011-970, Brazil
(wfl@inpa.gov.br)

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