

Impacts of roads and linear clearings on tropical forests

William F. Laurance^{1,2}, Miriam Goosem³ and Susan G.W. Laurance^{1,2}

¹School of Marine and Tropical Biology, James Cook University, Cairns, Queensland 4870, Australia

²Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Ancón, Panama

³School of Earth and Environmental Sciences, James Cook University, Cairns, Queensland 4870, Australia

Linear infrastructure such as roads, highways, power lines and gas lines are omnipresent features of human activity and are rapidly expanding in the tropics. Tropical species are especially vulnerable to such infrastructure because they include many ecological specialists that avoid even narrow (<30-m wide) clearings and forest edges, as well as other species that are susceptible to road kill, predation or hunting by humans near roads. In addition, roads have a major role in opening up forested tropical regions to destructive colonization and exploitation. Here, we synthesize existing research on the impacts of roads and other linear clearings on tropical rainforests, and assert that such impacts are often qualitatively and quantitatively different in tropical forests than in other ecosystems. We also highlight practical measures to reduce the negative impacts of roads and other linear infrastructure on tropical species.

Linear clearings in the tropics

Roads and other linear infrastructure such as power lines, gas lines, railroads and canals are among the most ubiquitous features of human activity, and are known to have important environmental impacts on natural habitats and ecosystems worldwide [1,2]. Such impacts appear to be particularly acute in tropical rainforests, for at least two reasons.

First, from a biological perspective, rainforests are characterized by a complex architecture and uniquely humid, dark, stable microclimate [3]. They sustain many species that are specialized for forest-interior and understory conditions, including some species that strongly avoid forest edges [4–9] and are unable to traverse even narrow forest clearings [10–13]. Other tropical species are susceptible to hunting, road kill, elevated predation and species invasions near roads. The net effect is that, by virtue of their unique characteristics and abundance of ecologically specialized species, rainforests and their biota are especially vulnerable to the environmental changes associated with roads and linear clearings [14].

Second, from a socioeconomic perspective, tropical rainforests largely occur in ‘developing’ nations, many of which are experiencing continued population growth, rapid economic development and intense natural-resource exploitation. In many developing nations, industrial logging, oil and gas development, agribusiness, mining and international donors and lenders are providing an

economic impetus for the expansion of road and infrastructure developments [15,16]. Roads and paved highways have a key role in opening up forested regions to exploitation from hunters, miners and forest colonists (Figure 1) [17,18], a problem exacerbated by often weak enforcement of environmental laws in remote frontier areas [19–21].

Here, we synthesize existing recent research on the impacts of roads and linear clearings on tropical rainforests and their wildlife. We examine linear infrastructure from various perspectives, demonstrating that its impacts are often qualitatively and quantitatively different in rainforests than in other ecosystem types. Practical measures to minimize or mitigate road impacts are also identified. Our synthesis is illustrated with research from the Amazon, Australasia, Central Africa and elsewhere in the tropics.

Impacts of roads and linear clearings

As summarized below, roads and other linear clearings can have an array of deleterious effects on tropical forests and their wildlife.

Physical disturbances

Linear infrastructure can have major impacts on local soils [22], hydrology and aquatic ecosystems [23]. Roads and highways, for example, are typically constructed using a cut-and-fill approach to help level local topography [2]. Unless frequent culverts are installed, filled areas impede drainage, especially in tropical regions that receive heavy wet-season rainfall. This can lead to extensive flooding on the upstream side of the road, killing large patches of inundated vegetation (Figure 2a). On the downstream side of road fills, water flow can be impeded, causing small streams to fail [1,2] and desiccation stress to vegetation, especially during the dry season. Road-cuts and local sand- and gravel-quarrying operations can also be major sources of erosion (Figure 2b) and stream sedimentation (from 35–500 tonnes ha⁻¹ yr⁻¹; [24]), further impacting aquatic ecosystems and biota and increasing the likelihood of landslides [22,25]. Additionally, tropical downpours, when concentrated through a few culverts into streams, can scour and channelize the streambed, simplifying aquatic habitats downstream [1,23]. Finally, roads can alter natural disturbance regimes: in fire-maintained tropical woodlands and savannas, for example, roads can create artificial firebreaks, leading to a proliferation of mesic vegetation at the expense of fire-adapted species [26].

Corresponding author: Laurance, W.F. (bill.laurance@jcu.edu.au).

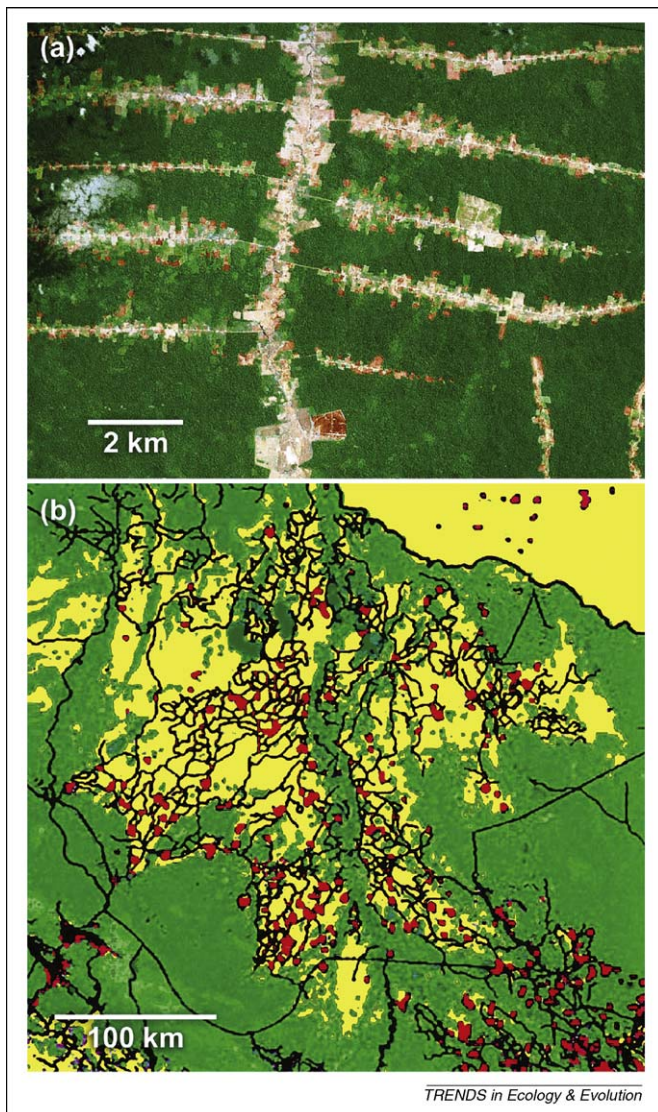


Figure 1. Roads and forest destruction. (a) Close association between frontier roads and deforestation in Brazilian Amazonia. (b) Concentration of forest fires (red) and deforestation (yellow) near roads in northeastern Bolivia during the 1997 El Niño drought. Intact forests are shown in green. Reproduced with permission from NASA (a) and M. Steininger, Conservation International (b).

Chemical and nutrient pollution

Roads and highways can be a large source of chemical pollutants. Dust, heavy metals, nutrients, ozone and organic molecules are often elevated within 10–200 m of road surfaces [1,27]. Lead pollution from car exhausts can be especially problematic, particularly in developing nations that still allow leaded gasoline [28]. However, de-icing salts, which can alter soil and aquatic chemistry and harm roadside vegetation [1], are not used in the tropics. Effects of chemical pollutants and nutrient runoff are likely to be especially serious for streams and wetlands near roads, with major pulses of waterborne pollutants and nutrients entering aquatic ecosystems with heavy rains at the onset of the wet season [29]. Such contaminants can have wide-ranging effects: for example, many aquatic invertebrates and vertebrates are sensitive to water pollution; waterborne nutrients can promote harmful eutrophication; and heavy metals are often biomagnified in aquatic food chains [1,27–29].

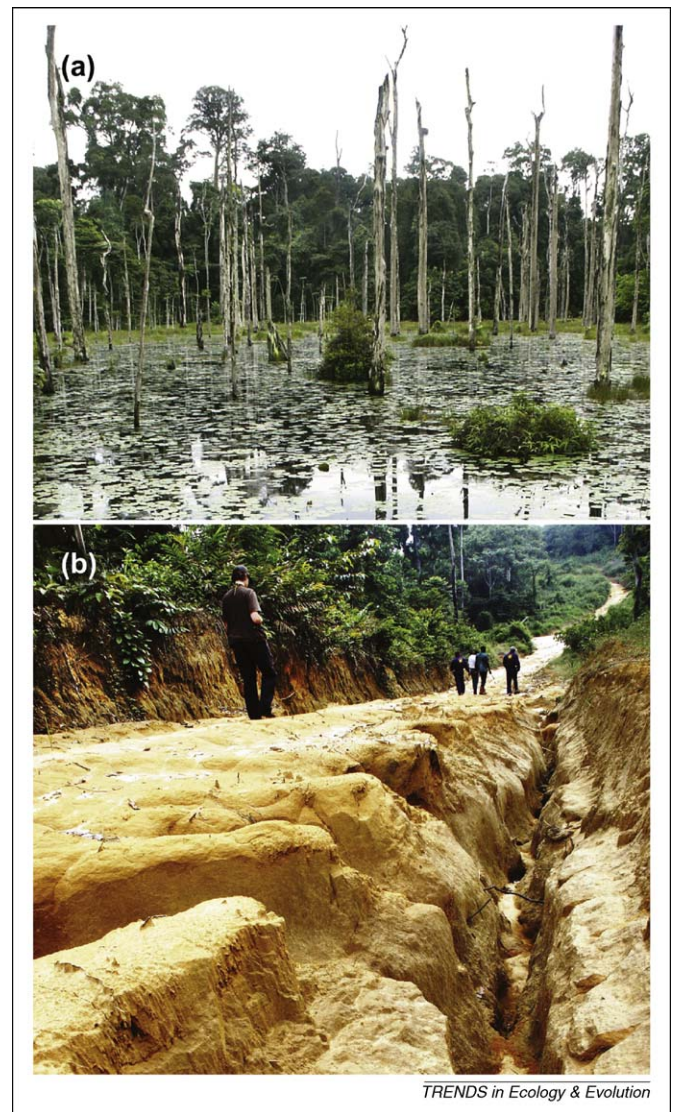


Figure 2. Dead trees from impeded drainage (a) and heavy soil erosion (b) along logging roads in Gabon, central Africa. Reproduced with permission from W. Laurance.

Edge effects

Edge effects are diverse physical and biotic changes associated with the often-abrupt verges of roads and linear clearings, and are particularly important in tropical rainforests [7,30]. Various edge-related changes in forest structure, microclimate and forest dynamics have been observed near linear clearings in the Amazon [7,31], the Caribbean [22], and tropical Australia [3,9]. For example, forests within 50–100 m of edges experience greater diurnal fluctuations in light, temperature and humidity [3], being typically drier and hotter than forest interiors, with elevated tree mortality, numerous canopy gaps and a proliferation of disturbance-adapted vines, weeds and pioneer species [7]. Such changes can alter the community composition and abundance of many different faunal groups [7–9,32–35].

The intensity of edge effects is influenced by the attributes of linear clearings. Clearing width is important, with narrow (<20-m width) linear clearings being less

vulnerable to edge-related wind disturbance and desiccation stress than are wider clearings [14]. The orientation of linear clearings with respect to solar angles can also influence edge-effect intensity [2,36]; clearings parallel to the solar track are exposed to sunlight throughout the day and, thus, are likely to suffer greater heat and desiccation at ground level than are those that are perpendicular to the path of the sun, which are fully insolated only at mid-day. Finally, the maintenance of linear clearings with herbicides, fires or cutting of foliage repeatedly disturbs the adjoining forest vegetation [6] and, by preventing natural edge closure, can cause edge effects to be elevated in intensity [3,7,30].

Road-related mortality

Some species suffer heavy mortality near roads from vehicle road kill (Box 1) [5,37,38], elevated predation [8] or human hunting [39–41]. If such effects are strong enough, the road could become a population sink, contributing to local extinctions of species [42]. Species that are rare, such as apex predators and large-bodied mammals and birds, and that require large home ranges or have low reproductive rates are generally most vulnerable to elevated mortality [43]. Paradoxically, although narrow forest roads facilitate road-crossing movements by animals, they also lead to greater road kill [5].

Road-related mortality can occur over varying spatial scales. Mortality from road kill and predation are generally limited to the road surface or adjoining road verges. Hunting by humans near roads, however, can create zones of elevated mortality and animal avoidance within at least 5–10 km of roads, and possibly much further for wide-ranging species, such as forest elephants and some primates [44–46]. Notably, the traits that predispose species to road kill (Box 1), such as slow movement, poor eyesight and edge-favoring behavior, are often different from those, such as large body size, gregarious social systems, conspicuous calls or displays and the use of regular pathways, that predispose them to hunting or trapping by humans [43,47]. Thus, roads have the potential to affect a broad spectrum of species with widely varying characteristics.

Barrier effects

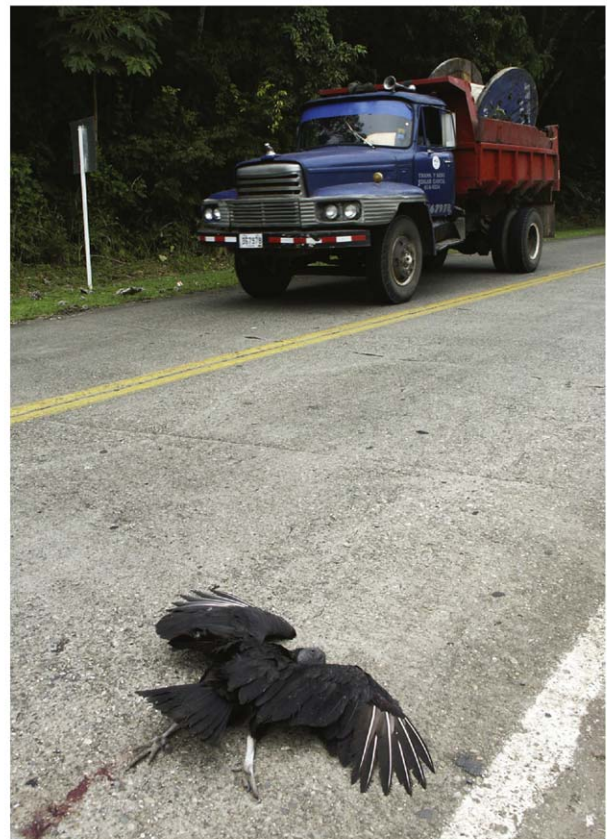
In some cases, roads and linear clearings can create barriers to faunal movements. One of the most striking features of tropical forests is the high proportion of species, including various beetles, flies, ants, bees, butterflies, amphibians, reptiles, birds, bats and small and large mammals, that tend to avoid even narrow (<30-m wide) clearings or forest edges [7–13,32–35,40,41,44–46,48,49]. Evidence for avoidance of edges and clearings comes from

Box 1. Vulnerability to road kill.

The locomotion, ecology and behavior of animals collectively determine their vulnerability to road kill by vehicles (Figure 1). Especially susceptible are: (i) slow-moving, ground-dwelling species, including many amphibians, reptiles and small mammals [5,9,98,99]; (ii) predominantly arboreal species that occasionally traverse open ground, such as tree-kangaroos, sloths and many primates [100]; and (iii) slower-flying birds, bats and insects with low flight paths [5,91,101]. Species with poor eyesight, including giant ant-eaters and tamanduas, and those that ‘freeze’ in response to approaching vehicles, such as armadillos, echidnas and many amphibians [102], are also vulnerable.

Road kill can also be heavy among: (i) reptiles that bask at night on warm road surfaces [5,38]; (ii) amphibians that undertake mass movements during tropical downpours [5,38,91,98]; (iii) species with key breeding or feeding sites near roads; (iv) dispersing or mate-hunting individuals [5,9,100]; (v) crepuscular species whose activity coincides with heavy morning and evening traffic; (vi) large animals, such as cassowaries, that must regularly traverse roads while ranging over extensive areas [102]; and (vii) species that forage along roads or road verges. The latter includes predators that favour forest edges and clearings, including certain hawks, bats and large carnivores [11,48,103,104]; owls and bats that prey on animals attracted or flushed by car headlights; herbivores browsing on forbs or grasses along road verges [105]; and scavengers feeding on road-killed carrion.

Road features also affect animal mortality. Road kill increases with high vehicle speeds and large traffic volumes [98,101,102], narrow road widths (which encourage road-crossing movements), and curves in roads (which reduce driver visibility and the response times of animals to oncoming vehicles) [5,11]. Incised topography and riparian vegetation tend to funnel amphibians, mammals and other animals into certain crossing routes, whereas steep slopes, cuttings and embankments tend to reduce road mortality by inhibiting road-crossing attempts [5]. If properly designed, bridges, culverts and underpasses reduce road kill by providing safe, alternate routes for road-crossing movements [6,14,60,90,91].



TRENDS in Ecology & Evolution

Figure 1. Road-killed vulture in Panama. Reproduced with permission from W. Laurance.

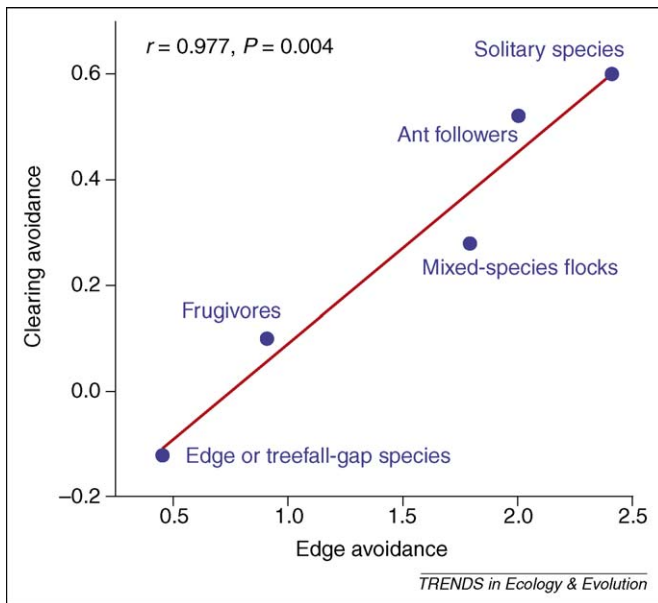


Figure 3. The association between indices of edge avoidance and clearing avoidance in guilds of Amazonian understory birds, showing that guilds that rarely cross road clearings also tend to avoid forest edges. Edge avoidance was the ratio of birds captured on mist-net lines far from (130 m) versus near (10–15 m) to road edges. Clearing avoidance was calculated as $(O-E)/E$, where O =observed rate of bird crossing for roads ~30 m in width, and E =expected rate of crossing based on movement frequency in intact forest. Adapted with permission from Ref. [11].

mark-recapture studies [8–11,13,32,33], experimental translocations [12,50], radiotelemetry [12,50] and field surveys [10,44,48] of various terrestrial vertebrates.

Notably, avoidance of forest edges and linear clearings appear to be strongly intercorrelated traits, at least for Amazonian birds (Figure 3) [11] and several Australian rainforest amphibians, skinks and small mammals [5], with both traits contributing to road-barrier effects. Avoidance of forest edges and clearings is believed to occur because tropical species: (i) have locomotor specializations, such as being strictly arboreal [50] or adapted for flying in dense, cluttered environments [48]; (ii) require dark, humid microclimates or specialized food resources [7–10,13,49]; (iii) exhibit strong psychological avoidance of clearings, presumably because of past selection pressures [8,11]; (iv) shun humans or traffic noise, light, movement and air pollution near roads [41,46,51]; (v) are repelled by invasive or generalist species in clearings [32,52,53] (*P. Byrnes, Honours thesis, James Cook University 2002*); and (vi) align their defended territories with clearing boundaries, thereby suppressing local movements by conspecifics [11,13]. In general, these traits are opposite to those that promote road kill (Box 1) because the latter results from attempted road-crossing movements [5,6,13].

Wider roads and highways can strongly hinder animal movements [5]. Among Amazonian understory birds, for example, translocated males (which are strongly motivated to return to their territory and mate) were able to cross a 75-m-wide highway but were entirely halted by a 250-m-wide clearing [12]. Similarly, in tropical Queensland, Australia, movements of native rainforest rodents (*Rattus* spp.) fell by 67–90% across narrow (6–12-m wide) clearings and by 90–100% across larger (20–60-m wide) clearings [13,32,33].

From a demographic and genetic perspective, a strong distinction exists between clearings that hinder animal or plant-propagule movements and those that prevent them completely [1,2]. Just one or a few successful migrants per generation are sufficient to prevent divided populations from diverging via genetic drift [54]. When populations are fully isolated, however, the deleterious effects of random demographic and genetic changes, in concert with environmental variations, can be a powerful driving force for local extinction [5,49,55]. According to some theoretical models, impeded dispersal alone might be sufficient to depress species richness near major highways [56]. Such deleterious effects are likely to be compounded as road density increases, with road-dominated landscapes (e.g. Figure 1a) becoming increasingly hostile terrain for sensitive species.

Exotic species invasions

Linear clearings are facilitating widespread species invasions in the tropics, for taxa ranging from little fire ants (*Wasmannia auropunctata*), exotic earthworms and non-rainforest vertebrates, to fungal die-back, caused by *Phytophthora* spp., and myriad weed species [32,52,53,57–60] (*P. Byrnes, Honours thesis, James Cook University 2002*). Some of these invaders are having major impacts on tropical biota. Little fire ants, for instance, are proliferating throughout African rainforests ~60-times faster along logging roads than through undisturbed forest, and are responsible for causing mortality or blindness in native species such as primates, leopards and many invertebrates [53]. Invasions can occur rapidly in tropical areas lacking seasonal restrictions on growth or movement; for example, non-rainforest frogs, leafcutter ants, lianas and exotic weeds are already penetrating remote areas of the Amazon, using the verges of recently constructed roads as invasion corridors [58]. Repeated spraying, burning or mowing of vegetation in linear clearings favors exotic and disturbance-adapted species at the expense of native species [59].

Road-borne invaders affect not only native biota in the tropics. In Ecuador, for example, levels of human enteric pathogens were 2–8-times higher in villages near roads than in more remote areas [61]. Likewise, increased incidences of dengue fever [62], malaria [63] and HIV [64] have been reported in people living near roads in India, Brazil and Uganda, respectively. By facilitating invasions of novel and potentially lethal pathogens, roads penetrating into remote frontier areas also pose a threat to indigenous groups attempting to live with limited or no contact with outsiders [65].

Human invasions

In the tropics, roads and highways often greatly facilitate invasions of hunters, miners, colonists and land speculators (Figure 1, Box 2), a phenomenon dubbed the ‘Pandora’s Box Effect’ [66]. In Brazilian Amazonia, for example, ~95% of all deforestation and fires occur within 50 km of highways or roads [15]. In Suriname, most illegal gold-mining operations are located near roads [67], whereas in tropical Africa, hunting intensity is so elevated near roads that it strongly affects the large-scale distribution of forest elephants, buffalo, duikers, primates and other exploited

Box 2. Roads and land-use dynamics.

In simplest terms, frontier roads are problematic because they distribute people broadly across the forest. Per-capita deforestation is inherently nonlinear (Figure 1), such that the first colonists arriving in an area destroy more forest per person than do later arrivals [96,106]. Thus, 1000 people in a single frontier village will destroy considerably less forest than will the same number of people living in ten scattered villages. By spreading people out across the forest, roads inherently promote rapid and widespread deforestation.

However, roads might also initiate more complex land-use dynamics. For example, in Laos [107], the Philippines [108] and Amazonia [97], landowners intensified agriculture close to newly constructed or improved roads at the same time that forest regeneration began in regions farther from the roads, often in upland areas, presumably because cultivators abandoned these lands or decided to work them less intensively [109]. In this sense, roads might sometimes act as 'magnets' for colonists, potentially reducing land-use pressures further afield.

Although few doubt that roads in virgin forests often cause serious environmental degradation, geographers and economists sometimes disagree about other types of road. In the Amazon, for instance, a heated debate has raged over plans to pave or expand existing roads in previously occupied areas, with some suggesting this could diminish net deforestation by concentrating people into already-degraded lands [97], and others arguing that it would cause deforestation to rise and spill-over into nearby forested areas [75]. Available evidence seems to favor the spill-over hypothesis (e.g. Refs [110,111]), suggesting that new roads are rarely beneficial for nature.

species [40,44–46]. Roads can also increase trade in bushmeat and wildlife products [17,18]; for example, on average, eight killed mammals were transported per hour along a single highway in Sulawesi, Indonesia [68].

Many formerly remote tropical regions such as the Amazon [65,69], Congo Basin [70], New Guinea [71] and Borneo [72] are now being assailed by expanding road networks, particularly from industrial timber operations and oil, gas and mineral projects [15,73]. Paved highways, which provide year-round access to forest resources and reduce transportation costs, typically have larger-scale impacts on forests and wildlife than do unpaved roads [15,20,74], which tend to become inaccessible during the wet season.

Reducing and mitigating the impacts of linear clearings

Various measures and design strategies can be used to curb the environmental impacts of roads and other linear infrastructure. These fall into two broad categories: local-scale efforts to reduce the impacts of new or existing linear clearings, and regional-scale efforts to limit their expansion into ecologically sensitive areas.

Limiting road expansion

In broad terms, roads can be thought of as the enemies of rainforests. Although essential in many cases for human activities and economic development, poorly planned or excessive road expansion can result in irreparable damage to, or destruction of, forests. Roads that penetrate into remote frontier regions often lead to forest encroachment and destruction (Table 1) and we recommend that these be avoided wherever possible. Paved highways are particularly damaging because they tend to spawn networks of secondary roads that can increase the spatial scale of their impact [75,76]; for example, the 2000-km-long Belem–

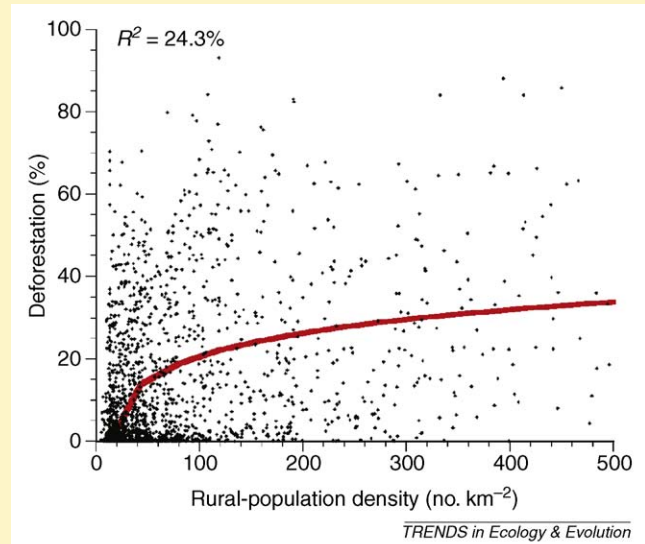


Figure 1. The nonlinear increase in forest loss with population density. Data shown are from 50-km × 50-km quadrats spanning Brazilian Amazonia. Adapted with permission from Ref. [96].

Brasília Highway, completed during the early 1970s, has now evolved into a 400-km-wide swath of forest destruction and secondary roads across the eastern Brazilian Amazon [66]. Efforts to project the long-term condition of Amazonian forests using an array of biophysical predictors suggest that the locations of highways and roads will be the greatest single factor influencing future spatial patterns of forest loss, fragmentation and degradation [15,74,77].

Large-scale efforts to expand regional highway networks in South America, South and Southeast Asia and, to an increasing extent, Sub-Saharan Africa, are cause for special concern. Across all of these regions, perhaps the most notable trend in recent years is growing investment by China in frontier roads, highways and railroads that will increase access to mineral and timber resources (Table 1). In general terms, maintaining large, roadless areas of intact forest should be among the highest priorities for regional conservation managers.

Managing timber operations

Industrial timber operations, which are currently occurring in ~28% of the tropical forests worldwide [78], are probably the greatest single driver of road expansion in forest frontiers. Many forests in the Asia-Pacific region have already been severely depleted by loggers. Surviving forests in the Amazon, New Guinea and Congo Basin are now undergoing rapid timber expansion, with the Congo alone having at least 52 000 km of recently created logging roads [70]. In the Amazon, forests penetrated by roads from selective logging operations are ~400% more likely to be deforested than are non-logged forests [79].

Most selective-logging operations in the tropics are poorly planned and have excessive road-building activities [80,81]. Ongoing efforts to reduce the ecological impacts of

Table 1. Examples of the most environmentally destructive roads in the tropics and others imminently planned or under construction.

Name and location ^a	Synopsis of impact
Existing roads	
Belem–Brasília Highway, Brazil	Completed in the early 1970s, this 2000-km highway has spawned a 400 km-wide slash of deforestation across eastern Amazonia
Cuiabá–Porto Velho Highway, Brazil	This 1500-km highway, funded by the World Bank, has promoted rampant forest loss in southwestern Amazonia
Cuiaba–Santarém Highway, Brazil	Visible as a ‘line of fire’ at night, this recently paved highway cuts into the heart of the Amazon for >1200 km
Ecuadorian oil roads	Roads associated with two 400-km-long oil pipelines have opened up much of Ecuadorian Amazonia to destructive colonization, with major impacts on indigenous groups
Samling Road, Sarawak, Malaysia	This 300-km road, recently built by Samling Timber Corporation, is opening up northern Sarawak, Borneo, to industrial logging
Andaman Trunk Road, Andaman Islands, India	Running 420 km across four nearby Andaman islands, this highway promoted massive deforestation and social upheaval for the indigenous communities of the islands
Douala–Bangui Road, Cameroon-Central African Republic	Completed in 2003, this highway cuts 1400-km across the northwestern Congo Basin and has promoted massive logging, poaching and forest loss
Roads under construction or planned	
Manaus–Porto Velho Highway, Brazil	This 900-km paved highway will link the almost pristine central Amazon to major population centres to the south
Transoceanic Highways, Peru-Bolivia-Brazil	Already hotspots of deforestation and frontier lawlessness, this triad of paved highways will link Brazil to the Pacific Ocean and lucrative export markets in China
Trans-Congo Road, Democratic Republic of Congo	Funded by China, this 1600-km road will cut across the Congo Basin, from the southeast to northwest, providing access to rich mineral and timber resources
North–South Economic Corridor, Indochina	This 1500-km highway will provide a direct link between aggressive timber importers in China and Laos, Cambodia, Thailand and Myanmar, whose forests are rapidly shrinking
Leuser Road Plan, Sumatra, Indonesia	This network of 450 km of main roads and 1200 km of minor roads is likely to open up surviving forests in northern Sumatra to illegal logging, poaching and deforestation
Mamberamo Basin Roads, Papua, Indonesia	Spanning 1400 km, this China-funded road network will traverse pristine forests in northwestern New Guinea

^aCompiled from refereed publications and technical reports and from consultations with tropical researchers (see Acknowledgements), environmental organizations and conservation websites such as <http://www.mongabay.com>.

selective logging operations focus strongly on roads, with measures such as: (i) minimizing roadworks via careful pre-harvest planning [82]; (ii) restricting roads to flatter slopes and ridgelines wherever possible; (iii) limiting widths of logging roads and loading ramps; (iv) minimizing stream crossings to reduce impacts on streams and riparian vegetation; and (v) prohibiting roading during wetter periods to reduce soil erosion and stream sedimentation [80,81]. In addition to these measures, more attention should focus on closing logging roads after harvest operations (e.g. by destroying key bridges or otherwise rendering the road impassable) to inhibit post-logging invasions of forests.

From an environmental perspective, some schemes for logging expansion appear particularly risky. In Brazilian Amazonia, for example, plans are being developed to log dozens of widely scattered National Forests, many located in remote, largely pristine areas, that could ultimately encompass over 50 million ha [83]. The network of new or improved roads required for such an enterprise could result in an array of undesirable consequences, such as facilitating hunting, forest invasions and land speculation in frontier areas. Although all approaches to logging

expansion have substantial environmental costs, roading impacts would be lower if logging were focused along existing highways and already-populated areas of the basin [84].

Reducing forest invasions

When roads in frontier areas cannot be avoided, uncontrolled forest loss and invasions can be reduced by creating protected areas (PAs) along the road route in advance of road expansion [77,85]. In the Brazilian Amazon, for example, forest destruction has been more severe along the Cuiabá–Santarém Highway, which had few PAs in place prior to road construction, than along the Porto Velho–Manaus Highway, where 13 PAs were established before or during road construction (although the latter is incompletely paved and could suffer further in the future; see <http://news.mongabay.com/2008/0926-amazon.html>). More generally, major forest fires are less frequent near roads in Amazonian PAs (including semi-protected reserves and indigenous lands) than near roads in unprotected forest (Figure 4) [86].

Another strategy to reduce invasions is establishing railroads rather than roads in frontier areas. Incursions into forests can be partially controlled because trains stop

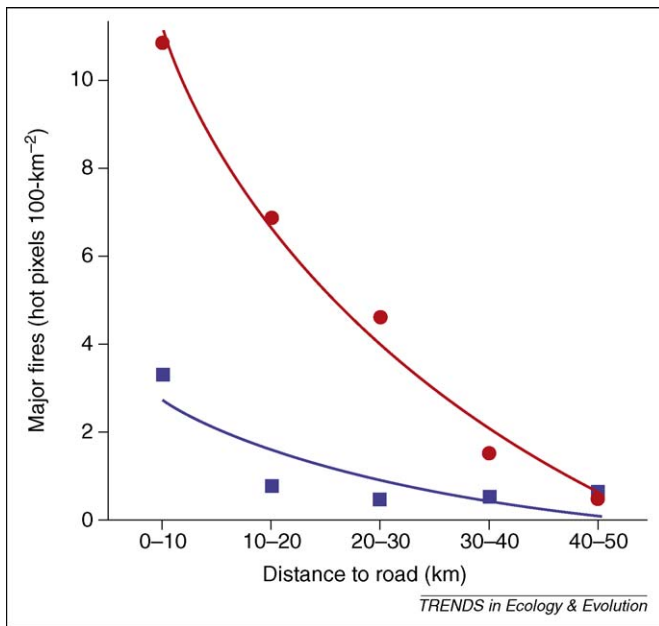


Figure 4. Incidence of human-lit forest fires at varying distances from roads, comparing areas inside (squares) versus outside (circles) protected areas in Brazilian Amazonia. Fitted curves are logarithmic. Adapted with permission from Ref. [86].

only at designated locations, and these can be situated strategically to limit invasions of environmentally sensitive areas. In Brazil, for example, a railroad has been advocated instead of the Manaus–Porto Velho Highway (see <http://news.mongabay.com/2008/0324-amazon.html>) because the highway could greatly increase forest colonization in central Amazonia (Table 1).

Oil and natural-gas pipelines are proliferating in many tropical regions [15,65,69], and the roads established for pipeline construction and maintenance often facilitate forest invasions. Although burying pipelines is moderately expensive, invasions can be reduced by such a measure and by allowing overlying forests to regenerate. This approach

has been adopted (but only incompletely implemented) for two major gas pipelines running from Camisea in the Peruvian Amazon across the Andes to the Pacific Ocean [65].

Properly assessing road impacts

Among the most serious hindrances to road mitigation is that, in many developing nations, environmental-impact assessments (EIAs) of roading operations focus solely on the road route itself, ignoring the impacts of roads on forest invasions, hunting, land speculation and secondary-road expansion [19–21,85]. In Brazil, for instance, EIAs of major new Amazonian highways were confined to a narrow swath along the road route itself, sometimes recommending such paltry mitigation measures as ‘helping’ animals to move from the planned route before road building [20,87]. In other cases, such as for certain mines, hydroelectric dams and other large developments, the EIA focuses on the project itself but ignores the impact that the roads will inevitably have [21,69]. New roads and highways will continue to be major drivers of rainforest loss and degradation so long as the EIA process is so fundamentally flawed [19–21,87].

Road-design strategies

In areas of high conservation significance, such as PAs and indigenous reserves, various measures can be used to reduce road and linear-clearing impacts. For nature reserves, roadworks and road density should generally be minimized, and roadless core-areas maximized, to sustain disturbance- and hunting-sensitive wildlife and reduce exotic-species invasions (e.g. Refs [39,45,46,59,88]).

Destructive flooding can be minimized and stream flows maintained by the establishment of large culverts under roads. These should be designed so that increased stream velocity within them does not create a barrier to aquatic fauna [89]. Soil erosion and stream sedimentation can be

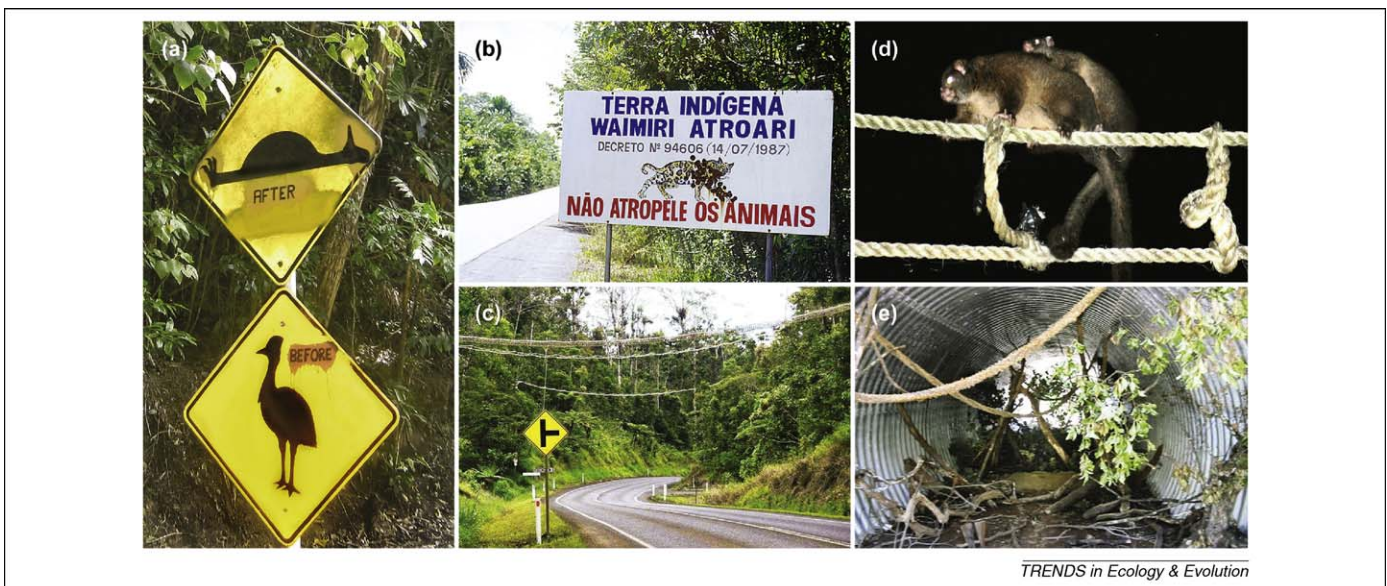


Figure 5. Efforts to mitigate road impacts: warning signs for motorists in tropical Queensland (a) and Brazil (b); artificial walkways for arboreal wildlife in Queensland (c), which enable road crossing by sensitive species such as the lemuroid ringtail possum (*Hemibelideus lemuroides*) (d); and wildlife-friendly culverts under roads in Queensland (e). Reproduced with permission from W. Laurance (a, b), M. Goosem (c, e) and J. Cooper (d).

reduced by confining the use of heavy equipment to drier months and by seeding fast-growing native plants over road cuts and disused quarry sites.

Edge effects along linear clearings can be reduced by allowing secondary growth and vines to proliferate along forest margins, road cuts and embankments, thereby providing a physical buffer that lessens forest desiccation and wind [3,7]. Minimizing road widths will also limit the 'fetch' of clearings, which influences wind- and microclimate-related edge effects. Mowing and brush cutting are generally superior to broad-scale herbicides and fire for controlling regrowth along clearing verges because they are less likely to damage regenerating forest-edge vegetation. Maintaining a relatively continuous canopy above roads reduces edge effects on microclimate and vegetation and helps to prevent invasions by weeds and associated exotic or non-rainforest fauna [6].

Barrier effects on wildlife can also be minimized by limiting road widths and maintaining a nearly-continuous canopy overhead [6], although such measures can increase road kill because road-crossing movements are more frequent [5]. Regrowth forest along road margins can further reduce the isolating effects of roads [8,11]. Bridges over watercourses that include a corridor of unflooded vegetation and natural streambed are especially effective for maintaining connectivity, both for terrestrial and aquatic fauna [6]. However, culverts and underpasses can provide effective avenues for movements of many animals, and can be designed to enhance their attractiveness to wildlife (Figure 5e) [90,91] and efficacy in reducing road kill [6,60]. Where maintenance of an intact canopy is infeasible, artificial canopy walkways can provide bridges for movements of many arboreal species in the tropics (Figure 5c,d), although their capacity to help sensitive fauna traverse wider (>30 m) clearings remains uncertain [60,91,92] (N.G. Weston, MSc thesis, James Cook University 2003).

Finally, road-kill mortality can be reduced by limiting vehicle speeds (via measures such as low legal speed limits, road-painting, warning strips and speed-bumps) [6,60], posting warning signs (Figure 5a,b), establishing wildlife fences along busy highways that help steer animals toward culverts and, in high-priority areas, by restricted night-time driving [93]. Most road kills occur at night and near dawn and dusk, when animal activity is highest [5,6]. In tropical Africa, restrictions on night-time driving within a PA have proven especially effective at reducing hunting activity [40].

Concluding remarks

Vulnerability of tropical forests

As detailed above, many of the impacts of roads and linear clearings appear to differ qualitatively or quantitatively between tropical rainforests and other ecosystem types. This occurs for at least five reasons.

First, rainforests have a complex, multi-layered architecture with dense canopy cover. This creates a dark, humid, thermally stable and nearly windless microclimate in the forest understory, which contrasts with harsher, more variable conditions in linear clearings. As a result of these strong physical gradients, edge effects are especially potent in the tropics.

Second, rainforests sustain numerous species with microhabitat, dietary and locomotor specializations. Such species tend to avoid linear clearings and forest edges or align their territories with clearing margins, increasing the likelihood of barrier effects, even when clearings are narrow (<30-m wide).

Third, intense tropical rainfall can exacerbate erosion and runoff from infrastructure projects, thereby increasing sedimentation and impacts on aquatic ecosystems. Linear infrastructure often impedes drainage, causing upslope flooding and desiccation of vegetation downslope. Furthermore, by concentrating heavy runoff into a few points, road culverts elevate stream velocity, which scours streambeds and simplifies downstream habitats. In this way roads can become barriers for aquatic fauna.

Fourth, where rainfall is seasonal, heavy metals and other pollutants can build up near the road surface during drier months. These are flushed into streams with the first heavy rains of the wet season, producing a potentially toxic pulse of pollutants when stream flow is still relatively low. Many species, such as fish, amphibians and freshwater invertebrates, are vulnerable to such pulses.

Finally, tropical forests mainly exist in developing nations, which are being transformed by ongoing industrialization, population growth and natural-resource exploitation. Roads and other linear infrastructure are rapidly expanding in many developing countries and have a key role in opening up forests to hunting, illegal mining, land speculation and destructive exploitation, a problem exacerbated by often weak enforcement of environmental laws in frontier areas. The proliferation of unplanned, illegal roads is a serious problem in many tropical nations.

A proactive approach

Efforts to promote road expansion in the tropics are perhaps the most striking example of how regional integration and economic development can be directly at odds with nature conservation. Whether in Africa, Asia or the Amazon, infrastructure planners typically extol the 'opening up' of new frontiers as a good thing (e.g. Refs [94,95]). Those alarmed by rapid environmental deterioration, however, usually see this in opposite terms given the logistical challenges, expense and, often, futility of frontier governance once the roads go in.

All is not lost, however. Given the central role of roads in promoting tropical deforestation and atmospheric carbon emissions [15,20,74], we assert that forest carbon-trading initiatives should often focus explicitly on limiting and mitigating frontier roads. For example, so-called REDD funds ('Reducing Emissions from Deforestation and Degradation'; see <http://unfccc.int/resource/docs/2005/cop11eng/102.pdf>) could be used to help plan and minimize regional road works, establish PAs in advance of road establishment, regulate road access, promote railroads rather than roads when feasible, and close down the most environmentally destructive roads. Such efforts might be more feasible than many realize. Although carbon trading will require that the impacts of planned roads on forest carbon stocks be projected with reasonable confidence, such impacts (including the influence of road paving, distance to population centers, land tenure and various biophysical

variables on deforestation dynamics) have been studied and modeled extensively (e.g. Refs. [15,65,69,73–75,79,96,97]).

Actively limiting frontier roads, we believe, is by far the most realistic, cost-effective approach to promote the conservation of tropical nature and its crucial ecosystem services. As Pandora quickly learned, it was much harder to thrust the evils of the world back into the box, than to simply not open it in the first place.

Acknowledgements

We thank M. Adeney, E. Bennett, S. Blake, T. Brooks, R. Butler, M. Cochrane, M. Cohen, P. Davidar, R. Ewers, P. Fearnside, T. Lovejoy, D. Neidel, D. Nepstad, C. Peres, A. Pfaff, S. Pimm, T. Rudel, N. Sodhi, M. Steininger, J. Supriatna, J. Vincent and three anonymous referees for information, imagery and insightful comments; L. Gonzalez for help with graphics; and James Cook University, the Australian Government's Marine and Tropical Sciences Research Facility and the Smithsonian Institution for support.

References

- Trombulak, S.C. and Frissel, C.A. (2000) Review of ecological effects of roads on terrestrial and aquatic communities, *Conserv. Biol.* 14, 18–30
- Forman, R.T.T. *et al.* (2002) *Road Ecology: Science and Solutions*, Island Press
- Pohlman, C.L. *et al.* (2009) Temporal variation in microclimatic edge effects near powerlines, highways and streams in Australian tropical rainforest, *Agr. For. Meteorol.* 149, 84–95
- Murcia, C. (1995) Edge effects in fragmented forests: implications for conservation, *Trends Ecol. Evol.* 10, 58–62
- Goosem, M. (1997) Internal fragmentation: the effects of roads, highways, and powerline clearings on movements and mortality of rainforest vertebrates. In *Tropical Forest Remnants, Ecology, Management, and Conservation of Fragmented Communities* (Laurance, W.F. and Bierregaard, R.O., eds), pp. 241–255, University of Chicago Press
- Goosem, M. (2007) Fragmentation impacts caused by roads through rainforests, *Curr. Sci.* 93, 1587–1595
- Laurance, W.F. *et al.* (2002) Ecosystem decay of Amazonian forest fragments: a 22-year investigation, *Conserv. Biol.* 16, 605–618
- Laurance, S.G. (2004) Responses of understory rain forest birds to road edges in central Amazonia, *Ecol. Appl.* 14, 1344–1357
- Goosem, M. (2000) Effects of tropical rainforest roads on small mammals: edge changes in community composition, *Wildl. Res.* 27, 151–163
- Develey, P.F. and Stouffer, P.C. (2001) Effects of roads on movements by understory birds in mixed-species flocks in Central Amazonian Brazil, *Conserv. Biol.* 15, 1416–1422
- Laurance, S.G. *et al.* (2004) Effects of road clearings on movement patterns of understory rainforest birds in Central Amazonia, *Conserv. Biol.* 18, 1099–1109
- Laurance, S.G. and Gomez, M.S. (2005) Clearing width and movements of understory rainforest birds, *Biotropica* 37, 149–152
- Goosem, M. (2001) Effects of tropical rainforest roads on small mammals: inhibition of crossing movements, *Wildl. Res.* 28, 351–364
- Laurance, W.F. and Goosem, M. (2008) Impacts of habitat fragmentation and linear clearings on Australian rainforest biota. In *Living in a Dynamic Forest Landscape* (Stork, N. and Turton, S., eds), pp. 295–306, Blackwell
- Laurance, W.F. *et al.* (2001) The future of the Brazilian Amazon, *Science* 291, 438–439
- Laurance, W.F. (2007) Forest destruction in tropical Asia, *Curr. Sci.* 93, 1544–1550
- Wilkie, D.S. *et al.* (2000) Roads, development, and conservation in the Congo Basin, *Conserv. Biol.* 14, 1614–1622
- Suárez, E. *et al.* (2009) Oil industry, wild meat trade and roads: indirect effects of oil extraction activities in a protected area in north-eastern Ecuador, *Anim. Conserv.* 12, 364–373
- Reid, J. and de Souza, W.D. (2005) Infrastructure and conservation policy in Brazil, *Conserv. Biol.* 19, 740–746
- Fearnside, P.M. (2007) Brazil's Cuiabá-Santarém (BR-163) Highway: the environmental cost of paving a soybean corridor through the Amazon, *Environ. Manage.* 39, 601–614
- Laurance, W.F. (2007) Road to ruin. *New Scientist*, 6 June, 25
- Olander, L.P. *et al.* (1998) Impacts of disturbance initiated by road construction in a subtropical cloud forest in the Luquillo Experimental Forest, Puerto Rico, *For. Ecol. Manage.* 109, 33–49
- Iwata, T. *et al.* (2003) Impacts of past riparian deforestation on stream communities in a tropical rainforest in Borneo, *Ecol. Appl.* 13, 461–473
- Bruijnzeel, L.A. (2004) Hydrological functions of tropical forests: not seeing the soil for the trees? *Agric. Ecosyst. Environ.* 104, 185–228
- Sidle, R.C. *et al.* (2006) Erosion processes in steep terrain – truths, myths and uncertainties related to forest management in Southeast Asia, *For. Ecol. Manage.* 224, 199–225
- Harrington, G.N. and Sanderson, K.D. (1994) Recent contraction of wet sclerophyll forest in the wet tropics of Queensland due to invasion by rainforest, *Pacific Conserv. Biol.* 1, 319–327
- Pratt, C. and Lottermoser, B.G. (2007) Trace metal uptake by the grass *Melinis repens* from roadside soils and sediments, tropical Australia, *Environ. Geol.* 52, 1651–1662
- García-Miragaya, J. *et al.* (1981) Lead and zinc levels and chemical fractionation in road-side soils of Caracas, Venezuela, *Water Air Soil Pollut.* 15, 285–297
- Pratt, C. and Lottermoser, B.G. (2007) Mobilisation of traffic-derived trace metals from road corridors into coastal stream and estuarine sediments, Cairns, northern Australia, *Environ. Geol.* 52, 437–448
- Gascon, C. *et al.* (2000) Receding edges and vanishing reserves, *Science* 288, 1356–1358
- Broadbent, E.N. *et al.* (2008) Forest fragmentation and edge effects from deforestation and selective logging in the Brazilian Amazon, *Biol. Conserv.* 141, 1745–1757
- Goosem, M. and Marsh, H. (1997) Fragmentation of a small mammal community by a powerline corridor through tropical rainforest, *Wildl. Res.* 24, 613–629
- Goosem, M. (2002) Effects of tropical rainforest roads on small mammals: fragmentation, edge effects and traffic disturbance, *Wildl. Res.* 29, 1–13
- Lehtinen, R.M. *et al.* (2003) Edge effects and extinction proneness in a herpetofauna from Madagascar, *Biodiv. Conserv.* 12, 1357–1370
- Watson, J.E.M. *et al.* (2004) Habitat structure and proximity to edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar, *Biol. Conserv.* 120, 315–331
- Pohlman, C.L. *et al.* (2008) Effects of severe tropical Cyclone Larry on rainforest vegetation and understory microclimate near a road, powerline and stream, *Austral Ecol.* 33, 503–515
- Novelli, R. *et al.* (1988) Study of birds killed by collisions with vehicles in a stretch of Highway BR-471, between Quinta and Taim, Rio Grande do Sul, Brazil, *Revista Brasileira Zool.* 5, 441–454
- Vijayakumar, S.P. *et al.* (2001) Herpetofaunal mortality on roads in the Anamalai Hills, southern Western Ghats, *Hamadryad* 26, 265–272
- Peres, C.A. and Lake, I.R. (2003) Extent of non timber resource extraction in tropical forests: accessibility to game vertebrates by hunters in the Amazon basin, *Conserv. Biol.* 17, 521–535
- Laurance, W.F. *et al.* (2006) Impacts of roads and hunting on central-African rainforest mammals, *Conserv. Biol.* 20, 1251–1261
- Laurance, W.F. *et al.* (2008) Impacts of roads, hunting, and habitat alteration on nocturnal mammals in African rainforests, *Conserv. Biol.* 22, 721–732
- Woodroffe, R. and Ginsberg, J.R. (1998) Edge effects and the extinction of populations inside protected areas, *Science* 280, 2126–2128
- Bennett, E.L. and Robinson, J.G. (2000) *Hunting of Wildlife in Tropical Forests: Implications for Biodiversity and Forest Peoples*, World Bank
- Lahm, S.A. *et al.* (1998) A method for censusing the greater white-nosed monkey in northeastern Gabon using the population density gradient in relation to roads, *J. Trop. Ecol.* 14, 629–643
- Blake, S. *et al.* (2007) Forest elephant crisis in the Congo Basin, *PLoS Biol.* 5, e111, DOI: 10.1371/journal.pbio.0050111

- 46 Blake, S. *et al.* (2008) Roadless wilderness area determines forest elephant movements in the Congo Basin, *PLoS One* 3, e3546, DOI: 10.1371/journal.pone.0003546
- 47 Bodmer, R.E. *et al.* (1989) Primates and ungulates: a comparison of susceptibility to hunting, *Primate Conserv.* 9, 79–83
- 48 Crome, F.H.J. and Richards, G.C. (1988) Bats and gaps: microchiropteran community structure in a Queensland rain forest, *Ecology* 69, 1960–1969
- 49 Laurance, W.F. (1991) Ecological correlates of extinction proneness in Australian tropical rainforest mammals, *Conserv. Biol.* 5, 79–89
- 50 Wilson, R.F. *et al.* (2007) Importance of canopy connectivity for home range and movements of the rainforest arboreal ringtail possum (*Hemibelideus lemuroides*), *Wildl. Res.* 34, 177–184
- 51 Dawe, G. and Goosem, M. Vehicle noise attenuation through tropical rainforest at ground and canopy levels: distance penetrated by noise disturbance. *J. Env. Manage* (in press)
- 52 Brown, G. *et al.* (2007) Toad on the road: Use of roads as dispersal corridors by cane toads (*Bufo marinus*) at an invasion front in tropical Australia, *Biol. Conserv.* 133, 88–94
- 53 Walsh, P.D. *et al.* (2004) Logging speeds little red fire ant invasion of Africa, *Biotropica* 36, 637–641
- 54 Slatkin, M. (1985) Gene flow in natural populations, *Annu. Rev. Ecol. Syst.* 16, 393–430
- 55 Lees, A.C. and Peres, C.A. (2008) Gap-crossing movements predict species occupancy in Amazonian forest fragments, *Oikos* 118, 280–290
- 56 Chave, J. and Norden, N. (2007) Changes in species diversity in a simulated fragmented neutral landscape, *Ecol. Model.* 207, 3–10
- 57 Dawson, P. and Weste, G. (1985) Changes in the distribution of *Phytophthora cinnamomi* in the Brisbane Ranges National Park between 1970 and 1980–81, *Aust. J. Bot.* 33, 309–315
- 58 Gascon, C. *et al.* (1999) Matrix habitat and species persistence in tropical forest remnants, *Biol. Conserv.* 91, 223–229
- 59 Goosem, M. and Turton, S.M. (2006) *Weed Incursions Along Roads and Powerlines in the Wet Tropics World Heritage Area*. Rainforest Cooperative Research Centre (http://www.rtrc.org.au/rfrcr/downloads/50_weed_incursions_full.pdf)
- 60 Goosem, M. (2008) Rethinking road ecology. In *Living in a Dynamic Forest Landscape* (Stork, N. and Turton, S., eds), pp. 445–459, Blackwell
- 61 Eisenberg, J.N.S. *et al.* (2006) Environmental change in the form of new roads affects the transmission of diarrheal pathogens in rural Ecuador, *Proc. Natl. Acad. Sci. U.S.A.* 103, 19460–19465
- 62 Dutta, P. *et al.* (1998) Distribution of potential dengue vectors in major townships along the national highways and trunk roads of northeast India, *Southeast Asian J. Trop. Med. Public Health* 29, 173–176
- 63 Hayes, J. and Ferraroni, J.J. (1981) Malaria along pioneer highways in the Brazilian Amazon, *Ciê. Cult.* 33, 924–928
- 64 Carswell, J.W. (1987) HIV infection in healthy persons in Uganda, *AIDS* 1, 223–227
- 65 Finer, M. *et al.* (2008) Oil and gas projects in the western Amazon: threats to wilderness, biodiversity, and indigenous peoples, *PLoS One* 3, e2932, DOI: 10.1371/journal.pone.0002932
- 66 Laurance, W.F. (1998) A crisis in the making: responses of Amazonian forests to land use and climate change, *Trends Ecol. Evol.* 13, 411–415
- 67 Laurance, W.F. (2008) The real cost of minerals. *New Scientist*, 16 August, 16
- 68 Lee, R.J. *et al.* (2005) Wildlife trade and implications for law enforcement in Indonesia: a case study from North Sulawesi, *Biol. Conserv.* 123, 477–488
- 69 Killeen, T.J. (2007) *A Perfect Storm in the Amazon Wilderness: Development and Conservation in the Context of the Initiative for the Integration of the Regional Infrastructure of South America (IIRSA)*, Conservation International
- 70 Laporte, N.T. *et al.* (2007) Expansion of industrial logging in Central Africa, *Science* 316, 1451
- 71 Shearman, P. *et al.* (2008) *The State of the Forests of Papua New Guinea*, University of Papua New Guinea and Australian National University
- 72 Curran, L.M. *et al.* (2004) Lowland forest loss in protected areas of Indonesian Borneo, *Science* 303, 1000–1003
- 73 Arima, E.Y. *et al.* (2005) Loggers and forest fragmentation: behavioral models of road building in the Amazon Basin, *Ann. Assoc. Am. Geogr.* 95, 525–541
- 74 Soares-Filho, B. *et al.* (2006) Modelling conservation in the Amazon basin, *Nature* 440, 520–523
- 75 Pfaff, A. *et al.* (2007) Road investments, spatial spillovers and deforestation in the Brazilian Amazon, *J. Reg. Sci.* 47, 109–123
- 76 Perz, S. *et al.* (2008) Road building, land use and climate change: prospects for environmental governance in the Amazon, *Phil. Trans. R. Soc. B* 363, 1889–1895
- 77 Nepstad, D.C. *et al.* (2006) Inhibition of Amazon deforestation and fire by parks and indigenous lands, *Conserv. Biol.* 20, 65–73
- 78 Asner, G.P. *et al.* A contemporary assessment of change in humid tropical forests. *Conserv. Biol.* (in press)
- 79 Asner, G.P. *et al.* (2006) Condition and fate of logged forests in the Brazilian Amazon, *Proc. Natl. Acad. Sci. U.S.A.* 103, 12947–12950
- 80 Putz, F.E. *et al.* (2000) Why poor logging practices persist in the tropics, *Conserv. Biol.* 14, 951–956
- 81 Fimbel, R. *et al.*, eds (2001) *The Cutting Edge: Conserving Wildlife in Logged Tropical Forests*, Columbia University Press
- 82 Picard, N. *et al.* (2006) Finding optimal routes for harvesting tree access, *Int. J. For. Eng.* 17, 35–49
- 83 Verissimo, A. *et al.* (2002) National forests in the Amazon, *Science* 297, 1478
- 84 Nepstad, D.C. *et al.* (2004) Managing the Amazon timber industry, *Conserv. Biol.* 18, 575–577
- 85 Fearnside, P.M. (2006) Containing destruction from Brazil's Amazon highways: now is the time to give weight to the environment in decision-making, *Environ. Conserv.* 33, 181–183
- 86 Adeney, J.M. *et al.* (2009) Reserves protect against deforestation fires in the Amazon, *Plos One* 4, e5014, DOI: 10.1371/journal.pone.0005014
- 87 Laurance, S.G. (2006) Rainforest roads and the future of forest-dependent wildlife. In *Emerging Threats to Tropical Rainforests* (Laurance, W.F. and Peres, C.A., eds), pp. 253–267, University of Chicago Press
- 88 Watts, R.D. *et al.* (2007) Roadless space of the conterminous United States, *Science* 316, 736–738
- 89 Pusey, B. *et al.* (2004) *Freshwater Fishes of North-Eastern Australia*, CSIRO Publishing
- 90 Goosem, M. *et al.* (2001) Will underpasses below roads restore habitat connectivity for tropical rainforest fauna? *Ecol. Manage. Restor.* 2, 196–202
- 91 Goosem, M. *et al.* (2006) Effectiveness of arboreal overpasses and faunal underpasses in providing connectivity for rainforest fauna. In *Proceedings of the 2005 International Conference on Ecology and Transportation* (Irwin, C.L. *et al.*, eds), pp. 304–316, North Carolina State University
- 92 Corlatti, L. *et al.* (2009) Ability of wildlife overpasses to provide connectivity and prevent genetic isolation, *Conserv. Biol.* 23, 548–556
- 93 Rajvanshi, A. *et al.* (2001) *Roads, Sensitive Habitats, and Wildlife: Environmental Guidelines for India and South Asia*, Wildlife Institute of India
- 94 Simuyemba, S. (2000) *Linking Africa Through Regional Infrastructure*, Economic Research Paper 64, African Development Bank
- 95 Duval, Y. (2008) *Economic Cooperation and Regional Integration in the Greater Mekong Subregion*, UN Economic and Social Commission for Asia and the Pacific
- 96 Laurance, W.F. *et al.* (2002) Predictors of deforestation in the Brazilian Amazon, *J. Biogeogr.* 29, 737–748
- 97 Weinhold, D. and Reis, E. (2008) Transportation costs and the spatial distribution of land use in the Brazilian Amazon, *Global Environ. Change* 18, 54–68
- 98 Aresco, M.J. (2005) Mitigation measures to reduce highway mortality of turtles and other herpetofauna at a north Florida lake, *J. Wildl. Manage.* 69, 549–560
- 99 Coelho, I.P. (2008) Roadkills of vertebrate species on two highways through the Atlantic Forest Biosphere Reserve, southern Brazil, *Eur. J. Wildl. Res.* 54, 689–699
- 100 Newell, G. (1999) Australia's tree-kangaroos: current issues in their conservation, *Biol. Conserv.* 87, 1–12
- 101 Rao, R.S.P. and Girish, M.K.S. (2007) Road kills: assessing insect casualties using flagship taxa, *Curr. Sci.* 92, 830–837

- 102 Moore, L.A. (2007) Population ecology of the southern cassowary, *Casuarius casuarius johnsonii*, Mission Beach, north Queensland, *J. Ornithol.* 148, 357–366
- 103 Colon, C.P. (2002) Ranging behaviour and activity of the Malay civet (*Viverra zibetha*) in a logged and unlogged forest in Danum Valley, East Malaysia, *J. Zool.* 257, 473–485
- 104 Dillon, A. and Kelly, M.J. (2007) Ocelot *Leopardus pardalis* in Belize: the impact of trap spacing and distance moved on density estimates, *Oryx* 41, 469–477
- 105 Vernes, K. *et al.* (1995) Home range characteristics and movement patterns of the red-legged pademelon (*Thylogale stigmatica*) in a fragmented tropical forest, *Wildl. Res.* 22, 699–707
- 106 Pfaff, A. (1999) What drives deforestation in the Brazilian Amazon? Evidence from satellite and socioeconomic data. *J. Environ. Econ. Manage.* 37, 26–43
- 107 Thongmanivong, S. and Fujita, Y. (2006) Recent landscape and livelihood transitions in Northern Laos, *Mountain Res. Devel.* 26, 327–344
- 108 Shively, G. and Martinez, E. (2001) Deforestation, irrigation, employment, and cautious optimism in southern Palawan, the Philippines. In *Agricultural Technologies and Tropical Deforestation* (Angelstam, A. and Kaimowitz, D., eds), pp. 335–346, CABI Publishing
- 109 Rudel, T.K. *et al.* Changing drivers of tropical deforestation create new challenges and opportunities for conservation. *Conserv. Biol.* (in press)
- 110 Geist, H.J. and Lambin, E.F. (2002) Proximate causes and underlying driving forces of tropical deforestation, *BioSci.* 52, 143–150
- 111 Chomitz, K.M. and Thomas, T.S. (2003) Determinants of land use in Amazonia: a fine-scale spatial analysis, *Am. J. Agric. Econ.* 85, 1016–1028