Fragmentation impacts caused by roads through rainforests

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Fragmentation is a severe threat to tropical rainforests. However the habitat loss and less extensive fragmentation caused by roads can also be a threat, not only through allowing access to remote areas, but also through a suite of insidious associated impacts. These include abiotic and biotic edge effects adjacent to road clearings, the disturbance impacts caused by vehicle operation, invasions by weeds, feral and alien fauna and disease, and faunal mortality from vehicle collisions. In combination, these can create a significant barrier to movements of rainforest biota. Impacts can be ameliorated through clever road design and sustainable vehicle operation.

Keywords: Edge effects, disturbance, fragmentation, rainforest, road.

THREATS to tropical rainforests related to clearing and fragmentation are well-documented[1,2], both for seasonal and aseasonal tropical rainforests. However, a less well-recognised threat is 'internal fragmentation' of remaining continuous and remnant forests where rainforest habitat is subdivided by internal clearings for highways, roads, railways, powerlines and pipelines[3]. Recent research has highlighted the impacts that road development through tropical forests potentially poses in term of a suite of consequential and often large-scale impacts, particularly in nations with developing economies. These include ingress by humans to otherwise remote forest areas with subsequent overhunting of wildlife[4–8] and unplanned or planned colonisation and clearing for agriculture and grazing[9–13]. Amidst this focus on larger-scale impacts, it should be recognised that road clearings also cause a suite of less obvious and insidious effects within the surrounding rainforest habitat, even when these areas are protected under conservation tenure[14,15]. The potential for loss of biodiversity caused by this group of impacts should not be underestimated.

Roads and other linear infrastructure for transport, energy and water supply are a basic requirement for economic development, providing necessary services for burgeoning human populations. However, they cause a variety of impacts during construction and operation. Environmental impacts of the operation of roads, highways and other linear clearings include loss of habitat caused by clearing; the alteration of habitat surrounding the clearing due to edge effects and disturbance by vehicle movement and emissions; the spread of weeds, feral animals, diseases and biota from other habitats; and mortality of fauna from collisions with vehicles. In combination, these effects can create a substantial impediment to movements of fauna and flora between habitats on either side of the clearing[14,15].

New highways and upgrades are currently proposed or under construction in many forested parts of Asia, including Borneo, New Guinea, China, India, and many South-East Asian countries that form part of the Asian Highway network. It may be possible to employ cost-effective measures to reduce the environmental impacts of these developments whilst maintaining the necessary economic gains, by applying the outcomes of recent road ecology research in Australian tropical rainforests[16]. In this article, I review the direct fragmentation impacts caused by roads through tropical rainforest, using examples from south-east and southern Asia where available, as well as tropical America and Australia. Secondly, I suggest principles and strategies for road design and operation which should ameliorate some of the impacts where roads traverse forested habitats.

Habitat loss

Roads and highways through forests result in substantial areas of habitat being cleared. For example, in the Wet Tropics World Heritage Area in northern Australia road clearings comprise about 3700 ha of roads in use and another 2000 ha which may be regenerating, covering about 0.5% of the total protected area[15]. In Meghalaya, India, as in many Asian protected areas, substantial areas (>450 ha) of reserved forests have been lost to roads[13]. In the United States, each kilometre of Federal Highway can alienate up to 13.5 ha of natural habitat[3]. However, edge and disturbance effects adjacent to roads and highways substantially increase the area of altered habitat.

Roads can significantly modify site hydrology and increase the likelihood of landslides[17], consequently affecting erosion, particularly on unsealed roads and resulting in sedimentation of streams. Increases in road runoff to streams can alter stream channels[17], changing stream bed and riparian habitats and impacting aquatic fauna[18,19].

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The worst erosion on unsealed roads in tropical rainforest areas occurs where tree canopy is lacking above the road surface rather than where canopy connectivity is maintained in multiple tree layers[20]. Stream water quality may also be diminished by pollutants in road runoff originating from vehicle emissions, lubricants, tyre and break wear, transport spillages and verge maintenance chemicals such as herbicides[21]. Contaminants in runoff from tropical rainforest highways include polycyclic aromatic hydrocarbons and heavy metals[22], with heavy metal contamination recognisable in downstream sediments as far as stream estuaries.

Edge effects

Edge effects comprise changes in the abiotic and biotic environment associated with the abrupt, artificial margins between natural habitat and a clearing[23]. Studies of edge effects along roads are few in comparison with those concerning fragments and continuous forests. However, road edges appear to cause comparably diverse impacts, although sometimes smaller in magnitude, depending on the width of the road clearing, the road surface composition and the vegetation matrix along the roadside[15]. Edge effects along linear clearings substantially increase the extent of habitat alteration in forest tracts[15], partly because each road section generates twice its length in forest edges.

Elevated light intensity and temperatures and increased moisture stress occur at the edges of rainforest roads and highways[24,25]. The severity and distance of penetration of these edge effects are modulated by (1) the width of the clearing and the consequent extent of canopy above the road surface[25]; (2) by the extent to which the edge is 'sealed' by vegetation filling the space between canopy and understorey after the edge is created[24], and (3) by the heat-storing qualities of the road surface[24]. As a result, an older, narrow, unsealed road with canopy stretching across the clearing and little disturbance of vegetation at forest edges will have far less severe and extensive microclimatic edge effects than a wide, paved highway lacking canopy over the road and a newly-created open edge or an edge kept open by continual grading, mowing or vegetation trimming along the road verge. Severity of microclimatic edge effects and their distance of penetration into the forest ranges between these two extremes, depending on road design and maintenance regimes (Figure 1).

Microclimatic alterations at road edges drive biotic changes in vegetation structure and floristics. Greater light availability, temperature extremes and increased moisture stress favour disturbance-adapted plants including weeds, wiry lianas and rainforest trees characteristic of early successional stages[26]. Similarly to edges of rainforest fragments[27], such conditions are stressful for trees of later successional stages, as evidenced by greater levels of branch fall and tree mortality[26]. This creates a feedback loop of greater canopy disturbance and thus greater light penetration and extremes of temperature and moisture stress. This change in vegetation floristics[26,28,29] at the edge is mirrored by alterations to vegetation structure. Overall abundance of trees at the edge increases, but the trees are smaller in diameter[26,28] and understorey is generally denser, lianas are less robust and woody vines are less common[26,28]. In some cases, there may be a link to roadside regeneration after clearing[8,28], but similar structural changes also occur in uncleared vegetation along linear clearings[26,30]. Where clearings are narrower and canopy is retained over the road surface, structure is less altered[31].

Under normal climatic conditions, gradients in wind speed from highway edges towards the forest interior are relatively minor[24]. Canopy vegetation damage resulting from severe cyclonic winds revealed no evidence for greater wind shear and turbulence near highway edges[32], unlike greater wind damage observed in Amazonia near the edges of forest fragments[27]. Instead severe damage occurred throughout the forest[32], with topographic ridge lines suffering most damage and no pattern adjacent to linear clearings. However, after the cyclone, the severe vegetation damage resulted in microclimatic extremes including wind speeds remaining elevated at much greater distances (at least 100 m) from the highway edge than prior to severe cyclonic damage (approx. 25 m)[32]. It is possible that road edge effects relating to wind shear damage could occur under less severe cyclonic conditions but, as yet, remains untested.

Alterations in microclimate, vegetation structure and floristics near roads affect rainforest faunal habitats and thus faunal abundances and species composition[8,14,28]. Near narrow, unsealed rainforest roads, alterations occur in abundances, diversity and species composition of small mammals[28,33–35], bats[36], understorey birds[37], entire bird communities[8,38], egg and seed predators[39], ants[29] and amphibians[40,41]. These community changes are similar to alterations observed in fragmented forests with distance of penetration being very variable and species- or guild-dependent. Certain species or groups tend to increase near roads (particularly edge or gap specialists and generalists), others are relatively unaffected, while many rainforest-dependent species decrease near the forest edge. In some areas, hunting pressure can contribute to a decrease in large species[8], while in other regions, anthropogenic faunal harvest may be less premeditated, through road mortality[3,42]. Avoidance of the open spaces associated with road clearings and the altered habitat of the forest edge is a common theme for rainforest-dependent birds including insectivores and mixed flocks[8,37,38], and is also seen for several small mammal species[33,35]. Conservative estimates of edge penetration (50 m) for Brazilian Amazonian understorey birds suggest that almost half a million hectares are edge affected for this group along the ~48,000 km of roads[37]. Avoidance is greatly reduced for

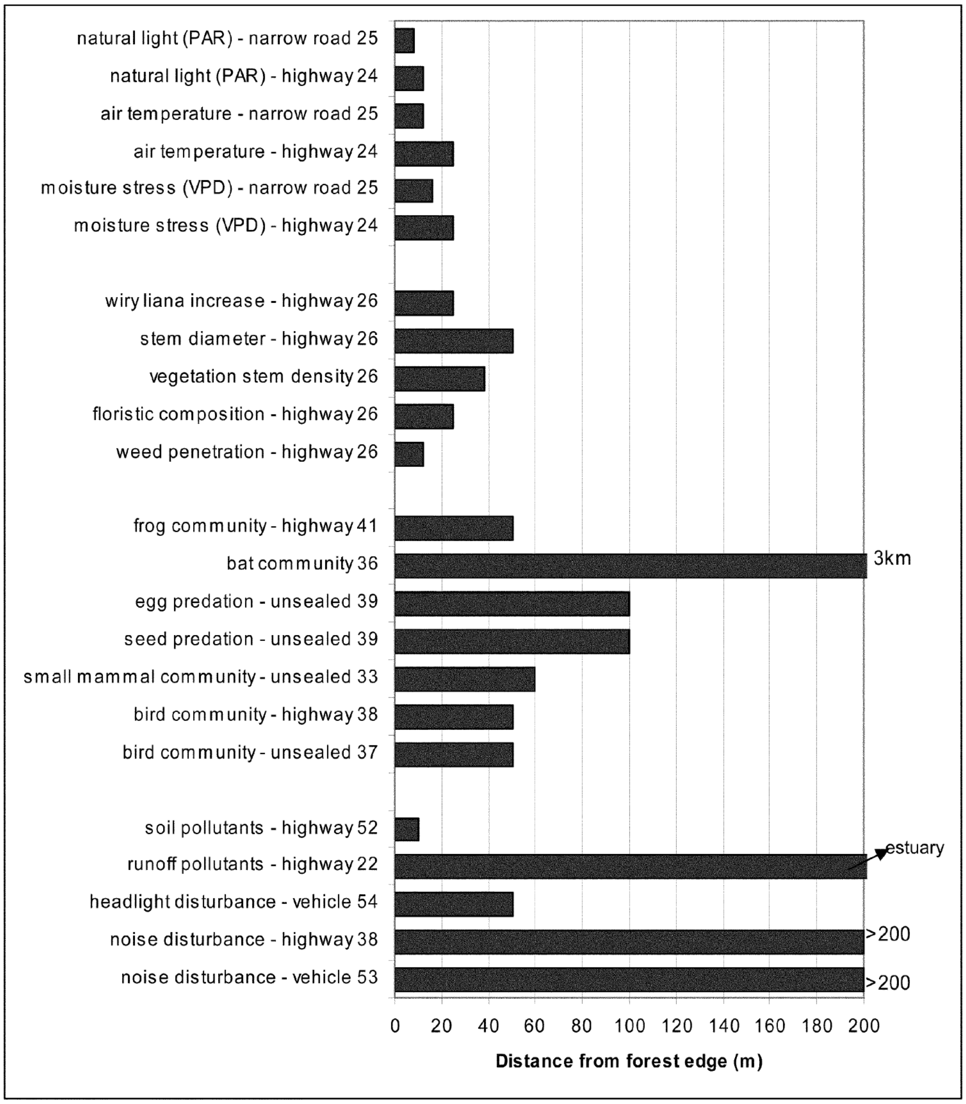

Figure 1. Extent of penetration of edge and disturbance effects from rainforest roads. Where distance of penetration was not listed by the author, the midpoint between distances demonstrating edge effects and distances without edge effects was used. Bar categories are followed by citation number.

certain small mammals by maintaining canopy above the road surface[33,35], or for some bird guilds, by allowing rainforest regrowth along road verges to buffer the forest edge, reducing alterations to edge microclimate and vegetation[37].

Disturbance effects

Road use causes disturbances from movement of vehicles which emit gas, liquid and solid pollutants as well as energy in the form of noise, headlights and vibration. Vehicles raise dust, particularly on unsealed roads, potentially reducing photosynthesis, transpiration and respiration in leaves[43,44], a problem well recognised in urban and temperate habitats, but seldom considered for rainforest vegetation[44]. Similarly, the impact of chemical pollutants arising from vehicle emissions[22] has not been reported for rainforest vegetation and fauna. In soils and roadside sediments adjacent to an Australian tropical rainforest highway carrying moderate traffic (~6000 vehicles/day), some heavy metals (Pb, Cu, Ni, Zn) and their bioavailability were elevated to levels considered contaminated[45]. High levels of heavy metal also occurred in roadside plants (Cu, Ni, Zn)[45], raising the risk of heavy metals bio-accumulation through the invertebrate and vertebrate food chain as seen in temperate zones[46–48]. Polycyclic aromatic hydrocarbons originating from exhaust gases and tyre wear, together with pesticides, herbicides and their associated surfactants that may be used for roadside maintenance, also can pose toxicity problems for amphibians at the concentrations potentially able to occur in road runoff or on roadsides[49–51]. However, heavy metal contamination of roadside soils generally does not extend very far through dense rainforest vegetation[45,52], in contrast to the great distances such contaminants can travel down streams from road runoff[22] (Figure 1).

Energy emissions from vehicles including noise and headlights can penetrate substantially to larger areas of rainforest than natural edge effects[38,41,53,54] (Figure 1). Such problems may be transitory on minor roads carrying low levels of traffic. However on major roads and highways such impacts can be almost continuous[38,41], although there may be lulls in nocturnal headlight and noise disturbance during the late evening and early morning hours, even on reasonably busy roads (>6000 vehicles/day)[41]. A range of faunal species are likely to be affected by such disturbance. Little is known about rainforest invertebrates other than the attraction of many species to fixed lighting such as street lights[54], whereas fireflies may avoid the interference caused by permanent lighting. Many insects use auditory communication[38], although the high frequencies used by groups including cicadas are unlikely to suffer interference from traffic noise[41]. Studies are not available regarding impacts of intermittent vehicle headlights upon rainforest vertebrates, although many species of mammals and amphibians are dazzled by lights, preventing normal vision for mammals for substantial periods of time[54], and probably increasing susceptibility to road mortality. Damaging physiological, psychological and behavioural alterations can follow both exposure to intermittent flashes of light, and the long-term changes to nocturnal habitat posed by street lights, to which animals such as bats and amphibians may be attracted for foraging, whereas others including many mammals avoid the surrounding altered habitat[54]. Many vertebrates are disturbed by traffic noise[38,41,55], with communication also affected for certain species. Particularly in rainforest birds[38] and amphibians[41], traffic noise can interfere with the frequencies used by some species for communication, potentially causing either avoidance of the road edge[38,41] or compensation through changes to loudness, pitch or number of calls used for communication[38,41], with likely deleterious impacts on energy budgets.

Invasions of alien flora, fauna and disease

Wide road verges of modified habitat provide potential sites for invasions of species alien to the surrounding rainforest, particularly roadsides that are managed to maintain low vegetation and without trees. Invaders can include weeds, feral fauna, and non-forest native fauna and flora. The dense closed canopy and low light penetration[24] means that rainforests are often relatively resistant to invasions[15] but roads and roadsides can become a conduit for movements of fauna and flora that can then penetrate deeply into otherwise relatively undisturbed forest tracts[30,56]. Road clearings facilitate weed invasions through several feedback loops. First, greater light availability allows establishment of light-requiring weeds including grasses and non-forest shrubs[30]. Secondly, these types of weeds can greatly impair ecosystem function as 'transformer species' that become self-perpetuating in roadsides. Grasses tend to promote fires[57] which kill rainforest seedlings, whereas dense thickets of woody, scrambling shrubs exclude recruitment of native trees and rainforest understorey, possibly also employing allelopathy to discourage establishment of other plants[30,58]. Thirdly, roadside maintenance practices including grading, mowing, vegetation trimming, herbicide spraying and removal of overhanging branches cause continuous disturbance and the high light conditions that favour weeds[14]. Finally, vehicles and people can be extremely effective propagule dispersers along open canopy clearings. For example, diseases such as plant dieback, *Phytophthora* spp., and the chytrid fungus that causes death in many frog species are both believed to be dispersed along roads and tracks in damp soil being carried by vehicles and on wheels and footwear[59,60].

Roads and altered habitat within verges allow fauna from other habitats to penetrate along the clearing and, in some cases, invade the rainforest itself. Roads are recognised conduits for many species[61]. Well-known examples include the cane toad, *Bufo marinus*, which invades new areas in most habitats via roads[62], and which occasionally penetrates rainforest although preferring the road and its verge[41,42,63]. Carnivores also travel along roads[64], with feral cats and dogs moving along narrow rainforest roads in north-eastern Australia[65], and feral pigs using the clearing for movement and foraging[65,66]. Road verges can provide habitat for entirely separate faunal communities from those inside the rainforest. For example, in north-eastern Queensland, grassland and feral small mammals colonise and dominate the wide verges of narrow unsealed rainforest roads which lack canopy above the road capable of preventing domination of the verge by tall grasses and woody weeds[33–35,67]. Similarly, ant[29] and bird[8,37] communities are altered in road verge habitat that is dissimilar to interior forest.

Road mortality

One of the more obvious impacts of roads traversing rainforest is the toll of fauna killed in collisions with vehicles. Vertebrates killed are estimated at about 1000–3000 per km annually on a rainforest highway carrying about 4000 vehicles/day in north-eastern Queensland, Australia[3,42,68]. Amphibians dominated the annual toll of vertebrates, forming about 75% of the victims[3,42], whereas mammals and reptiles comprised about 12.5% each. Numbers of victims recorded on a separate highway were proportional to the lower traffic levels[69]. Insect casualties also demonstrate dependence on traffic volumes[70]. However, road mortality is not always related to the amount of traffic that the road carries. In the case of minor roads carrying low levels of traffic at night, traffic volume may have little effect, as nocturnal species in particular may have ample opportunity to safely cross the road[34].

A variety of other factors also influence patterns of mortality on rainforest roads. Behavioural traits, such as mass migrations by amphibians to breeding ponds[71] are implicated in road mortality in many habitats, however mass migrations are uncommon in rainforests. Instead, species-dependent and seasonal behaviours such as breeding in roadside drains by amphibians[14], basking on the road surface by reptiles[72] and seasonal reproduction and juvenile dispersal in small and arboreal mammals[3,42,73], predispose individuals to rainforest road mortality. Foraging scavengers are a frequent victim in open habitats, although unexpectedly less common along some rainforest roads[42]. Mammalian carnivores[64] and other species that use roads for normal diurnal and/or dispersal movements may also be susceptible[63]. Nocturnal fauna including many amphibians[74] and mammals[54], when dazzled by headlights, remain immobile on the road surface in response to an approaching vehicle. Other species avoid mortality due to behaviours such as flying above the vehicle zone[54,70], arboreal species using canopy connections for crossing[55] or terrestrial species demonstrating speed or intelligence in avoiding vehicles[3,42].

Spatial influences on the degree of mortality of different species include aspects of road design and landscape features. The width of clearing for the road and its verge affects road mortality of many rainforest species. For amphibians and small mammals in north-eastern Australian rainforest, as the road clearing width increases, road mortality decreases[3,42]. This avoidance of open spaces by species adapted to rainforest[3] is a behaviour that becomes more prevalent with increasing traffic speeds[42]. Features in the landscape including creeks and gullies form a natural conduit for animal movements that encourage animals to cross where they intersect with the road. The result can be road kill aggregations both in continuous rainforest[3,42], and particularly in cleared landscapes where rainforest has been retained forming a riparian corridor[67]. Conversely, road design features that create a physical barrier to movements such as steep road cuttings and embankments tend to reduce casualties[42], unless animals become trapped on the road surface adjacent to such features and cannot escape quickly, as observed for tree-kangaroos in north-eastern Queensland (pers. obs.).

The impact of this unpremeditated harvest of individuals from tropical rainforest animal populations is currently unquantified, although surmised to be serious in the case of threatened species and species that are particularly susceptible to road kill. Certainly, a variety of amphibians[75], reptiles[76] and mammals[77] appear to suffer declines adjacent to roads in temperate zones. Populations of endangered and rare rainforest species such as cassowaries[78] (14% of known adults killed in three years) and tree-kangaroos[73] (road kills formed 10% of observed individuals) are considered threatened by the levels of road mortality which they suffer in north-eastern Australia. In extreme cases such as these, road mortality could create a population sink on roads and highways carrying high traffic volumes continuously or at times of day or seasons when species are especially vulnerable[14].

Roads as barriers to movement

As a result of the combination of this variety of road impacts, roads, their verges and the adjacent edge- and disturbance-affected rainforest habitat can form substantial linear barriers to road crossings for many rainforest species. This internal fragmentation within continuous forest could cause similar problems regarding population and genetic isolation as traditional fragmentation of habitat remnants within a cleared agricultural matrix, albeit probably not as severe for the majority of species[15,79]. Barrier effects can lead to loss or reduced efficacy of ecosystem processes including pollination and dispersal that rely on faunal movement. Similarly to road mortality, the degree to which linear barrier effects operate is dependent on species behaviour as well as road design features and landscape aspects. Species that are highly disturbed by noise, headlights or other vehicle emissions and those rainforest specialists that avoid the altered structure and microclimate of forest edge habitats are most at risk of barrier effects that restrict or prevent attempts to cross the road. Crossings of species which avoid open spaces in clearings may also be severely restricted, even without avoidance of edge habitats and vehicular disturbance[80,81]. A third group of species at high risk of isolation by roads comprises those that do not avoid open clearings or disturbed edge habitat but instead are so vulnerable to vehicles that no individual succeeds in crossing the road[14].

The width of the clearing and thus the distance of open area required to be crossed is particularly pertinent to the degree of barrier effects experienced by many animals. Birds of the Amazonian rainforest understorey, particularly those of certain insectivorous guilds and those occurring in mixed flocks, avoid crossing open road clearings, even when the road carries minimal traffic[8,79,80], avoiding both the gap in the canopy caused by the road clearing, and, in many cases, also avoiding edge habitat[80]. Similarly, small mammals demonstrate greater avoidance of crossings of wide rainforest road clearings than narrower road clearings[67,82]. The habitat present in the road verge, analogous

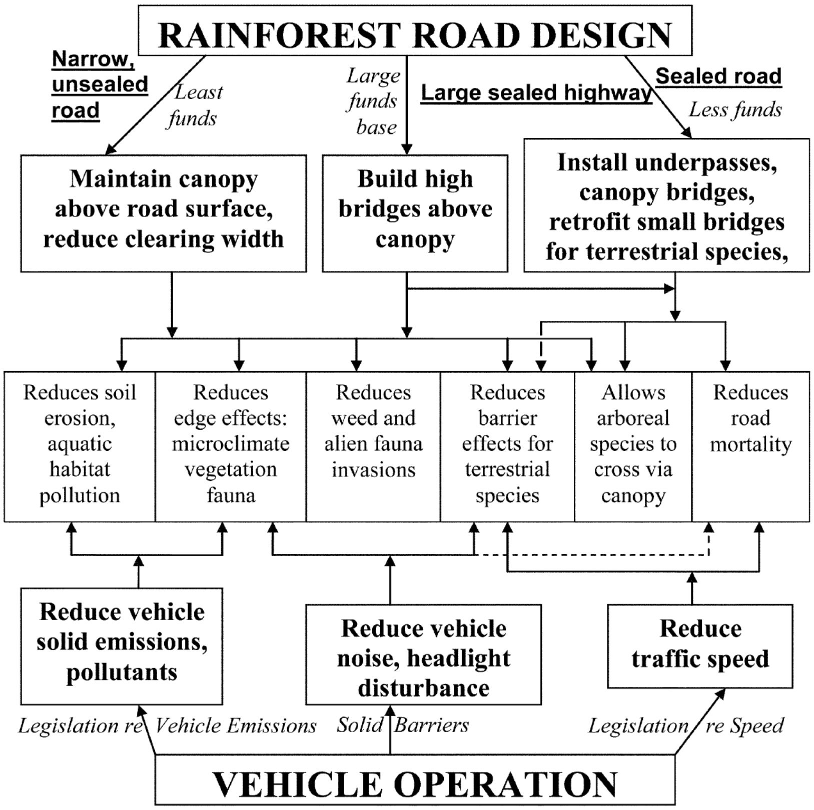

Figure 2. Amelioration of impacts of operation of rainforest roads ranging from narrow, unsealed roads to large highways. Types of road are underlined, strategies to achieve reduction of impacts shown in boxes in bold, impacts addressed in boxes in regular font, resources required in italics.

to the matrix between rainforest remnants, can mediate against or increase this avoidance. Particularly when there is tall regrowth in the road verge, or closed canopy above the road surface, movements across roads are much more common amongst the rainforest groups studied[35,80,83], whereas a grassy or weedy verge causes greater crossing inhibition[35]. Obligate arboreal vertebrates are often loath to come to ground level for the purposes of crossing open road gaps, thereby making this group particularly vulnerable to fragmentation effects where no canopy connections exist above the road surface[55]. Terrestrial vertebrate groups which appear to avoid crossing road gaps include microhylid frogs and several specialised rainforest skinks[42]. These species do not move quickly in comparison to vehicles, do not have alternative routes for road crossing, and yet are not road victims, suggesting they could be suffering severe barrier effects.

Reducing road impacts

These spatial and temporal patterns of road fragmentation impacts suggest a suite of principles to take into consideration during design of road upgrades. Several amelioration strategies can potentially mitigate against more than one road impact simultaneously (Figure 2). The most suitable mitigation techniques will depend upon the type of road (unsealed vs sealed vs large highway), the amount of funding available and the reason that the work is being undertaken (upgrade vs new construction). A separate suite of impacts related to vehicle operation can be considered for legislative attention. These include simple measures such as setting lower maximum traffic speeds and if feasible in the economic climate, reducing emissions from vehicles, including chemical pollutants, noise and restricting headlight types. Both legislative approaches should reduce edge and barrier effects for fauna, whilst lower traffic speeds should also reduce road mortality. The introduction of solid barriers along highway edges, although an expensive option for many situations, can reduce noise and headlight problems for terrestrial fauna, although these emissions may be deflected towards the canopy at reduced intensities. However, the provision of such barriers may also increase the physical barriers posed to crossing movements of fauna, unless other strategies are also incorporated into road design.

The cheapest and easiest technique to decrease fragmentation effects and particularly suitable for narrow, unsealed roads and sealed roads carrying low traffic volumes, involves maintaining canopy above the road surface[14,69]. A suite of impacts are decreased including barrier, edge and weed invasion effects together with soil erosion and thus aquatic habitat sedimentation due to unsealed roads (Figure 2). This amelioration is easily achieved by road maintenance practices that only remove dead or dangerous branches and avoid grading, mowing or spraying of road verges once canopy cover is established. However, this technique will not decrease road mortality, so is unsuitable for roads carrying heavy traffic loads.

For heavy-use highways when funding is available, high, long bridges over streams that provide wide, undisturbed riparian strips are the best option for reduction of barrier effects for terrestrial species[14,69] (Figure 1). If these are built at sufficient height to straddle the canopy, arboreal fauna will also have unimpeded movement. Coupled with a fencing strategy for the remainder of the road, fauna can be encouraged to move below the road, thus also avoiding road mortality. Edge, invasion and erosion impacts along the riparian strip are also avoided, although disturbance from traffic noise, headlights and pollutants will continue to be a problem. Embankment and cutting width should be minimised using reinforcements such as gabions and revegetation to reduce overall clearing width and minimise edge effects along the remainder of the road. Included within such a design, purpose-built faunal underpasses or modified culverts can provide further habitat connectivity. If arboreal species need to be considered, canopy bridges may be trialled to determine effectiveness.

Road upgrades with limited funding that carry intermediate traffic loads may consider a variety of retrofitting options including ledges within culverts for terrestrial faunal use and cheap rope canopy bridges to reduce barrier effects for arboreal fauna. Maintenance practices should reduce clearing width and encourage tree growth along road verges to the degree possible within safety margins. Should endangered fauna be present, fencing that funnels fauna towards underpasses and culverts should be considered to prevent mortality. The majority of these approaches to amelioration can be achieved at minimal cost.

Conclusions

Roads cause a variety of fragmentation impacts within rainforest. These include habitat loss and alterations, edge and disturbance effects, invasions and road mortality. In combination, these changes can create a substantial barrier to movements which can subdivide populations of fauna and flora, fragmenting the forest biota and associated ecological processes. Amelioration strategies for these impacts range from high-cost bridges for mega-highways which can reduce almost all impacts other than habitat loss and alteration from edge effects and disturbance, through low-cost retrofitting of culverts and careful maintenance practices to almost cost-free maintenance of canopy for narrow unsealed or sealed roads carrying low traffic volumes.

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