The Ecological Implications of Roads

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1. Summary

Roads are an important and necessary part of everyday life for most people, forming the basis of the overland transportation network (along with railways) in nearly all countries. Road development influences a wide range of phenomena, from human society, business and economies, to the natural environment (Forman *et al.* 2003). In regional development, roads are often perceived as the initial stage of development, especially in tropical areas where they open access to remote areas for colonisation, agricultural development, and resource extraction (Laurance *et al.* 2001, Arima *et al.* 2005, Perz *et al.* 2007, Caldas *et al.* 2010). Roads further facilitate development by providing market access for rural producers, integrating economic sectors and reducing the cost of spatial mobility (Perz *et al.* 2007).

Global road networks have been expanding at a rapid rate since the 1900's (Forman *et al.* 2003), making roads a distinctive feature in any landscape, with many countries giving 1-2% of their land surface over to roads and roadsides (Forman 1998). In many emerging economies, road building is vital for stimulating and maintaining economic growth (Andersen & Reis 1997). Today the highest rates of road expansion can be seen in the developing tropics and in emerging economies, where roads are given high priority by governments to encourage growth and reduce poverty through increasing spatial connectivity, aiding travel, helping establish land claims and facilitating the extraction of resources (Munnell 1992, Calderon & Serven 2004, Straub 2008, Perz *et al.* 2012). Indeed roads are expanding at rapid rates across the tropics, for example, on average 17,000 km of roads are added to the Brazilian Amazon each year (Ahmed et al. 2013).

Despite the irrefutable socio-economic benefits that roads bring to humans, they often result in negative impacts on the environment (Forman & Alexander 1998, Spellerberg 1998, Fahrig & Rytwinski 2009, Laurance *et al.* 2009, Perz *et al.* 2012). The ecological effects of

roads spread far beyond the physical footprint of the network and may impact 15-20% of the surrounding land (Forman & Alexander 1998). The ecological effects of roads are diverse, ranging from road mortality events, loss of habitat, the formation of barriers to animal dispersal and gene flow, to, altering habitat structure, creating edges, introducing pollutants, changing hydrological processes and increasing susceptibility to alien invasion (Forman & Alexander 1998, Keller & Largiader 2003, Laurance *et al.* 2004, Shyama Prasad Rao & Saptha Girish 2007, Jaeger *et al.* 2005). These effects vary across biomes, habitats and scales. Many road impacts eventually cause changes to biodiversity richness and species composition (Wilkie *et al.* 2000, Forman *et al.* 2003, Spooner & Smallbone 2009).

One of the most striking road effects is the impact roads have on deforestation in tropical regions. In the context of tropical deforestation, roads cause a relatively small amount of direct habitat loss, but exert a huge indirect influence on the spatial patterns of deforestation by allowing easier access to new frontiers (Fearnside 2008, Geist & Lambin 2002, Perz *et al.* 2007, Perz *et al.* 2008). Roads also encourage extractive industries and further deforestation by settlers, thereby indirectly influencing deforestation rates.

This report aims to outline and provide details on the key ecological implication of roads.

2. Background

Since the 1900's, global road networks have been expanding at a rapid rate (Forman *et al.* 2003). Road networks were first studied by 'transportation geographers' (Coffin 2007) whose main concerns were structural network properties, economics and development. From this early work a number of quantitative methods were developed for the study of networks (Coffin 2007), yet little attention was given to the environmental impacts that the road networks had. One impact however, namely road mortality, has been at the forefront of research on road effects from as early as 1935 (Stoner 1935).

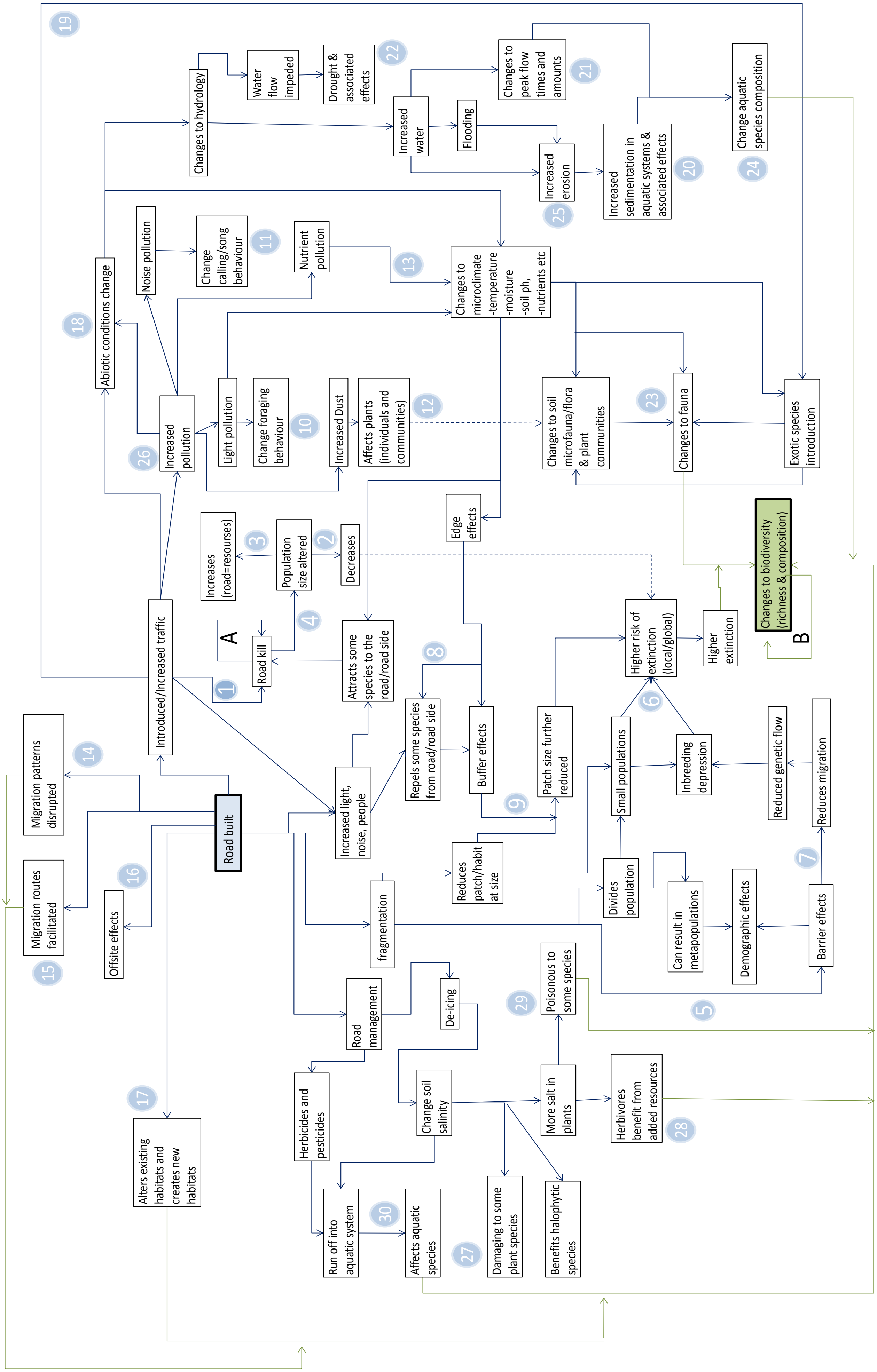
By the 1970's, research on the effects of roads on 'wildlife' began to emerge in earnest, with work centring on three main topics: 1) road mortality; 2) roads as barriers; and 3) roads inducing behavioural changes in animals. In the 1980's, the field of landscape ecology began to establish (Wiens *et al.* 2007), and with it came a strong focus on the effects of scale and fragmentation patterns. Given roads are a major force in fragmenting natural habitats, it is unsurprising that in recent years attention has been turned towards the effects of roads on landscapes and ecology, and has even led to the emergence of a new field coined 'Road Ecology' (Forman 1998). This research field focuses on understanding the interactions between road networks and the natural world, and is growing.

Roads have many and varied ecological effects, many of which are difficult to categorise into discrete themes. Most often, ecological effects fall into multiple categories or there are associated knock on effects and links between categories (Figure 1). Some road effects act at large scales over long periods of time, such as traffic pollution that has long term implications for climate, whereas other effects have more localised and short term impacts such as isolated incidences of road mortality. The magnitude of the ecological impacts are determined by a range of factors, including: (1) the scale of the road or road network (physical size); (2) the level of use (traffic flow) with a busy road likely to have a larger impact than a quiet one; and (3) the time of road use which will moderate the magnitude and target of the impacts. For instance, if traffic is highest at night, nocturnal animals may suffer more than diurnal animals. Geographic location also plays a role in determining the ecological impacts of roads. For example, pollutants from de-icers will be an issue in cold regions but irrelevant in hot regions, creating a latitudinal gradient in the nature of road impacts. At a smaller spatial scale, roads on the side of hills vs those on flat land will have different impacts on hydrology and erosion rates.

Impacts from roads often occur beyond the immediate vicinity of the roads themselves, impacting much greater spatial areas than might be expected from the size of the network alone. The extent and direction in which road impacts are transmitted beyond the physical boundary of a road can be highly variable. Some effects occur far from the road itself, such as the quarrying and manufacture of road-building materials, whereas impacts such as road mortality are tightly constrained to the location of the road itself. In between these two extremes lie buffer effects, which shadow the spatial pattern of road networks but extend beyond the road itself, such as light pollution from road lights. Buffer effects, also called the ‘road-effect zone’, extend variable distances from the road edge depending on the specific effect (Forman & Deblinger 2000, Coffin 2007). Some road effect zones are directional, with hydrological changes and erosion patterns having knock-on effects that are transmitted downstream and downhill, but probably not upstream or uphill. Roads also cause changes to abiotic processes, which in turn can influence biotic responses. For example, roads through forests can create open edges that have increased exposure to the sun and altered microclimates, which in turn can cause a shift in animal and plant distributions.

Some ecological impacts are incremental and cumulative, with the impact growing as the road network grows or as the road is in operation for longer. For example, the spatial area impacted by edge effects will increase as the road network grows over time. By contrast, some effects may be felt only in the short term, such as a pulse of sediment into streams during the road building process. Importantly, road effects can change with the life of the road; the effects during the construction, operation, maintenance and de-commissioning or abandonment phases of a road will all differ. In a similar vein, some effects are incidental, arising as a result of people using roads for purposes other than what they were initially constructed for. For example in Africa, roads built to extract timber for the forestry industry are used by people to gain access to forest for hunting bush meat (Wilkie *et al.* 2000).

The variety of effects and the fact that roads impact more of an ecosystem than would be indicated by their physical footprint (much like a keystone species impacts its environment more than expected) means that roads could be considered ‘keystone landscape elements’ (McGarigal *et al.* 2001). The rest of this section is an overview of the breadth and extent of road effects. It serves to illustrate why roads are important in understanding environmental changes and why it is important to model them.


Road built
Introduced/Increased traffic
Road kill
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Population size altered
Increases (road=resourses)
Decreases
Attracts some species to the road/road side
Increased light, noise, people
Repels some species from road/road side
Increased pollution
Light pollution
Change foraging behaviour
Noise pollution
Change calling/song behaviour
Nutrient pollution
Increased Dust
Affects plants (individuals and communities)
Abiotic conditions change
Changes to hydrology
Water flow impeded
Drought & associated effects
Increased water
Flooding
Changes to peak flow times and amounts
Increased erosion
Increased sedimentation in aquatic systems & associated effects
Change aquatic species composition
Changes to microclimate -temperature -moisture -soil ph, -nutrients etc
Changes to soil microfauna/flora & plant communities
Changes to fauna
Exotic species introduction
Edge effects
Buffer effects
Changes to biodiversity (richness & composition)
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Higher risk of extinction (local/global)
Higher extinction
Patch size further reduced
Small populations
Inbreeding depression
Reduced genetic flow
Reduces migration
Reduces patch/habit at size
fragmentation
Divides population
Can result in metapopulations
Demographic effects
Barrier effects
Migration patterns disrupted
Migration routes facilitated
Offsite effects
Alters existing habitats and creates new habitats
Road management
De-icing
Herbicides and pesticides
Change soil salinity
More salt in plants
Poisonous to some species
Herbivores benefit from added resources
Run off into aquatic system
Affects aquatic species
Damaging to some plant species
Benefits halophytic species
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Figure 1. Major ecological effects of roads, how they are linked and how they affect biodiversity. Loops, (A) Road kill attracts scavengers resulting in more road kill, (B) changes in species richness and composition has knock on effects via food webs and species interactions that result in further diversity/composition changes, these changes may be subject to time lags (Findlay & Bourdages 2000). **Figure citations**; (1) Stoner 1935, Forman & Alexander 1998, (2) Kociolek *et al.* 2011, (3) Kristan *et al.* 2004, (4) Fahrig &Rytwinski 2009, (5) Keller & Largiader 2003, (6) Caughley 1994, (7) McGregor *et al.* 2008, (8) Lehman *et al.* 2006, (9) Coffin 2007, (10) Rydell 1992, (11) Brumm 2004, Slabbekoon & Ripmeester 2008, (12) Farmer 1993, (13) Angold 1997, (14) Sawyer *et al.* 2005, (15) Trombulak & Frissell 2000, (16) Spellerberg 2002, (17) Lugo & Gucinski 2000, (18) Spellerberg 2002, Forman & Alexander 1998, (19) Forman & Alexander 1998, Parendes & Jones *et al.* 2000, (20) Jones *et al.* 2000, (21) Jones *et al.* 2000, (22) Trombulak & Frissell 2000, Laurance *et al.* 2009, (23) Fagan *et al.* 1999, (24) Bain *et al.* 1988, (25) McGarigal *et al.* 2001, (26) Bingal *et al.* 2007, (27) Spellerberg 2002, (28) Laurian *et al.* 2008, (29) Mineau & Brownlee 2005, (30) Sanzo & Hecnar 2006.

3. Ecological Effects

3.1 Road mortality

Mortality is one of the most obvious, and one of the first road effects to be studied, with the literature dating from the 1930's (Stoner 1935, Scott 1938). These recordings were primarily concerned with large mammals and tended to present observations of mortality (Stoner 1935, Scott 1938, Pickles 1942). Even today the literature is primarily concerned with vertebrates (Shyama Prasad Rao & Saptha Girish 2007). More recently, the effects of road mortality on populations and demography have moved the field from empirical observations to predictive modelling (Row *et al.* 2007, Clevenger *et al.* 2003, Jaeger *et al.* 2005, Jaarsma *et al.* 2006, Ortowski 2008, Glista *et al.* 2009, Roger *et al.* 2010). Road mortality directly reduces population size, however, for most species, the loss of individuals through road mortality is not a significant determinant of population survival (Adams & Geis 1983, Munguira & Thomas 1992, Forman & Alexander 1998, Hels & Buchwald 2001, Seiler *et al.* 2004, Orlowski & Nowak 2006, Munro *et al.* 2012). This, however, depends on the frequency of deaths and specific species traits (Hodson 1962, Fahrig & Grez 1996, Carr & Fahrig 2001, Barthelmess & Brooks 2010, Caceres 2011, Rytwinski & Fahrig 2011). Species with low population densities and/or low reproductive rates will be more severely impacted than species with high reproductive rates and population sizes, because the loss of each individual has a higher impact on the overall population. Florida Scrub Jay (*Aphelocoma coerulescens*) (Mumme *et al.* 2000), Audubon's Crested Caracara (*Polyborus plancus*), the Hawaiian Goose (*Branta sandvicensis*) (Kociolek *et al.* 2011), Barn owl (*Tyto alba*) (Fajardo 2001), Little owl (*Athene noctua*) (Hernandez 1988), Spotted turtle (*Clemmys guttata*) and Blanding turtle (*Emydoidea blandingii*) (Beaudry *et al.* 2008) are examples of species that do suffer population declines as a result of road related mortality.

Road mortality events can be beneficial to some species. Species that eat road kill, such as ravens and vultures (Kristan *et al.* 2004, Kelly *et al.* 2007), and which have the capacity to avoid traffic, show an increase in abundance and thus benefit from road mortality events (Fahrig & Rytwinski 2009). For example, carrion eaters take advantage of road kill, which may be seen as a diet subsidy. Common ravens (*Corvus corax*) that have a greater content of road kill in their diet have greater fledgling success (Kristan *et al.* 2004). Further, a survey of the foraging behaviour of 1,947 ravens found that 21 % of all feeding and foraging behaviour was related to road kill events (Dean & Millton 2003).

3.2 Fragmentation

Roads can fragment habitats and act as barriers to dispersal; they present a disjunction in habitat that that many animals avoid crossing. This impact may be magnified by road mortality (forming an 'absorbing' barrier), but in most cases the avoidance is behavioural with species avoiding the road itself. For some species, roads are 'absolute' barriers that are never crossed (Keller & Largiader 2003), although for many species the road forms a semi-permeable barrier that individuals actively avoid crossing. Crossing avoidance has been observed across many taxa including, mammals (Richardson *et al.* 1997, Dyer *et al.* 2002, Rico et al 2007, McGregor *et al.* 2008), birds (Laurance *et al.* 2009, Tremblay & St Clair 2009), amphibians (Marsh *et al.* 2005), reptiles (Shepard *et al.* 2008) and invertebrates (Keller & Largiader 2003, Bhattacharya *et al.* 2003).

Road avoidance behaviour affects species' distribution resulting in, range shifts, range restrictions and changes in habitat use, by acting as barriers or buffers. The Moustached monkey (*Cercopithecus cephus)*, Grey-cheeked monkey (*Lophocebus albigena)*, Agile mangabey (*Cercocebus agilis),* Amur tigers (*Panthera tigris altaica*), Elephants (*Loxodanta africana cyclotis),* Red duikers (*Cephalophus* spp.), Oven birds (*Seiurus aurocapillus*) and Woodland salamanders (eg *Plethodon metcalfi*) are all encountered significantly less near roads (Ortega & Capen 1999, Kerley *et al.* 2002, Potvin *et al.* 2005, Whittington *et al.* 2005, Blom *et al.* 2005, Semlitsch *et al.* 2007). In some cases this is a result of the road itself, for example with woodland salamanders that avoid logging roads even once they have been abandoned (Semlitsch *et al.* 2007). In other cases avoidance occurs as a result of the positive relationship between roads and other human pressures such as hunting for example with wolves (Whittington *et al.* 2005) and in some cases avoidance is because roads reduce habitat quality (Ortega & Capen 1999).

The level of road avoidance, and therefore the level of impact that road induced fragmentation might have on a population, is determined by the interaction of species traits with road characteristics. Species with large territories, species that are easily disturbed by light and noise, and species that use habitat cover for movement, are more impacted by road fragmentation. A small or narrow road is less of a barrier than a large or wide road, as evidenced by studies on carabid beetles (Yamada *et al.* 2010), understory birds of the Amazon (Goosem 2007, Laurance *et al.* 2009), small mammals (Goosem 2007, Rico et al 2007) and obligate arboreal vertebrates (Gossem 2007). The difference in impact can be large, with data from small rodents crossing forest roads showing that movement rates across roads were reduced by 67-90% across narrow clearings and by 90-100% across wide clearings (Laurance *et al.* 2009). Concomitant with road width is traffic density which also influences the permeability of a road barrier. For example, Chruszcz *et al.* (2003) found that Grizzly bears (*Ursus arctos)* are more likely to cross roads with low traffic density. For other species, traffic density has no effect because animals are avoiding the road itself, because it is an open, vulnerable location, rather than avoiding the various emissions from vehicles, such as light and noise (Rico *et al.* 2007, McGregor et al 2008). The degree of road avoidance can be further modulated by intra-specific trait variation. For example, female panthers (*Puma concolor*) avoid road crossings, but male panthers readily cross roads (Kerley *et al.* 2002).

For some species the presence of individual roads is not a deterrent, but the overall density of the road network is a key determinate of habitat selection. Grizzly bears (*Ursus arctos)* (McLellan & Shackleton 1988, Mace *et al.* 1996), elk (*Cervus elaphus roosevelti*) (Witmer & deCalesta 1985), wolves (*Canis lupus*) (Thiel 1985, Mech *et al.* 1988, Whittington *et al.* 2005, Potvin *et al.* 2005) and amphibians (Vos & Chardon 1998, Eigenbrod *et al.* 2008), all preferentially locate in areas of lower road densities. This could be because areas of low road density areas experience less human impact and disturbance. In fact, road density was found to be more important than forest cover for habitat choice in three frog species; *Bufo americanus, Rana pipiens* and *Hyla versicolor* (Eigenbrod *et al.* 2008).

Road networks gradually build up over time, and as a result shifts in species' ranges are considered cumulative effects (Whittington *et al.* 2005). A region that previously did not have a road density high enough to force certain species to avoid it can find those species progressively excluded as road density increases. However, despite many animals exhibiting a negative relationship with road density, some animals benefit from high road densities. White-footed mice (*Peromyscus leucopus)* avoid road crossing but the negative impacts of this seem to be outweighed by a positive effect on their abundance near roads. Rytwinski & Fahrig (2007) suggest two possible reasons: (1) roads are positively correlated with an undetermined component of habitat quality; or (2) roads negatively impact White-footed mice predators.

Fragmentation results in smaller suitable habitat patches, which inevitability have lower carrying capacities than large habitat patches, resulting in reduced population sizes. Further, roads act as barriers to movement, resulting in these smaller populations being isolated (if the road is an absolute barrier) or establishing metapopulations (if there is some movement across the roads). Either way, small populations are at greater risk of extinction as a result of stochastic demographic and environmental shifts (Caughley 1994). Roads reduce re-colonisation of empty habitats by limiting immigration (McGregor *et al.* 2008), and that increased isolation reduces gene flow, which combined with small population sizes, can result in inbreeding depression.

As roads fragment habitat, they create edges leading to edge effects; defined as the ecological effects arising as a result of interactions between adjacent habitats that are separated by a transition zone that is usually abrupt (Murcia 1995). Road building typically creates new edge effects because the road presents a new environment that is juxtaposed with, or more usually passes through, an existing habitat. Roads induce drastic abiotic edge effects along their borders, which include changes to the microclimate; light levels generally increase, air and soil temperature and moisture change because of increased exposure, soil pH and nutrient levels change because of roadside management and the introduction of a road surface which is chemically different to the native habitat (Delgado et al 2007, Honu & Gibson 2006, Gehlhausen *et al.* 2000). Changes to abiotic conditions can have knock on effects, for example forest edges along roads tend to be drier than forest areas with no roads, and as such they are more prone to fire (Cochrane & Laurance 2002).

Changes in the abundance of species (Marsh & Beckman 2004, Donovan et al 1997, Lehman et al 2006), distribution of species (Lehman *et al.* 2006, Baldi & Kisbenedek 1999) and introduction of alien species (Honu & Gibson 2006) can all occur as a direct result of edges being present and changes in abiotic conditions near the edge. The spatial scale of road induced edge effects increase over time as the network grows. Further, road edges are different to naturally formed edges because eventually they 'box in' a patch (i.e. they form around the patch perimeter). This boxing in is particularly problematic as the network grows because patches become smaller with the effective patch size being further reduced by buffer effects. As a result of the negative effects of road induced fragmentation, strategies attempting to mitigate these effects have been made, including, over- and under-passes, corridors, canopy bridges and areal stepping stones (Colcheo *et al.* 2011, Taylor & Goldingay 2011, Goosem 2012, Lesbarreres & Fahrig 2012).

3.3. Behaviour

Roads fragment habitats and reduce animal movement, alter species ranges and the habitat selection patterns of individuals. All of these effects are mediated by animal behaviour or, most specifically, road avoidance behaviour. Conversely, species that benefit from roads might be attracted to habitats near or containing a high density of roads. The distributions of the Turkey vulture (*Cathartes aura*) and Black vulture (*Coragyps atratus*) are influenced by the distribution of carrion such as road kill (Kelly *et al.* 2007). Raptors (Accipitridae and Falconidae) are attracted to roads because, although they tend not to feed on road kill, they are attracted to the productive road-side verges that are often good habitats for small prey (Dean & Millton 2003). Kangaroo rats (*Dipodomys ordii*) benefit from easier digging, dust bathing and higher seed banks found along road edges (Stapp & Lindquist 2007). Basking lizards and snakes take advantage of the increased temperature of tarmac (Vijayakumar *et al.* 2001). Herbivores may also be attracted to road side habitats where vegetation has higher concentrations of salts and nutrients, usually from de-icers, fertilizers and other road side pollutants. For example, moose (*Alces alces*) generally avoid roads but are attracted to roadside vegetation along roads that are de-iced with salt, because the plants contain a higher level of sodium, which can be a limited resource (Laurian *et al.* 2008).

Roads may also alter migratory patterns, with some animals avoiding routes near roads but others making use of the easier path that a road offers as a movement corridor. For example, Mule (*Odocoileus hemionus*) and Pronghorn deer (*Antilocapra Americana)* experience bottlenecks in their migration routes as a result of roads and housing developments (Sawyer *et al.* 2005) and it is thought that the building of a new road in the Serengeti will result in disruption to Wildebeest migration (Dobson *et al.* 2010). Conversely caribou (*Rangifer tarandus*) utilise cleared winter roads in the direction of their normal migratory pattern (Trombulak & Frissell 2000). Cane toads (*Bufo marinus*) and wolves have also been shown to utilise roads as movement corridors (Brown *et al.* 2006, Forman *et al.* 2003). Species that utilise roads for movement may gain access to previously unoccupied habitats and thus expand their range.

Road lights, light from passing vehicles and the way light ‘interacts’ with the road, can all deter or attract animals, causing changes to normal behaviour. Light pollution is one of the most rapidly increasing changes to the environment (Cinzano *et al.* 2001). Approximately two thirds of the world’s population and 99 % of the European Union population are in areas where the night sky is above the threshold for light polluted status. Large areas of natural and semi-natural areas are exposed to light pollution from nearby urban areas and roads (Santos *et al.* 2010). Illumination from roads could be seen as more invasive than that from urban areas because roads and their associated light penetrate into natural habitats. Artificial illumination from roads parallel to beaches (and beach front developments) causes disorientation in baby sea turtles, who orient themselves towards the sea by using patterns of light reflected from the sea (making it brighter) and absorbed by the beach/vegetation behind the beach (Tuxbury & Salmon 2005, Santos *et al.* 2010). Fledglings of sea birds also experience disorientation from artificial light as they attempt to reach the sea for the first time (LeCorre *et al.* 2002), and many die as a result of injuries, starvation or predation, because of failure to reach the water quickly (Santos *et al.* 2010).

Light pollution from roads and roadsides can also have positive impacts on some species. Nocturnal predators experience greater visibility for hunting and others can feed upon concentrations of insects that are attracted to lights (Rydell 1992). Large numbers of congregated insects provide an ideal foraging location for insectivorous bats (providing they are able to avoid traffic). A study by Rydell (1992) showed that the gross energetic intake of *E. nilssonii* foraging around road lights was more than twice as high as those foraging in wood lands (0.5kJ/min compared to 0.2kJ/min) as a result of lights attracting energy rich moths (as opposed to flies in woodlands). Diurnal animals may extend their daily activity as a result of the extra light.

Road surfaces can interact with natural light, mimicking cues and signals that some insects rely on for normal mating behaviour. Mating and egg-laying mayflies (Ephemeroptera) are attracted to asphalt roads because reflected light is strongly, horizontally polarised, which makes it appear like a water surface to insects that seek water based on polarotaxis (partial and horizontal polarisation of reflected light). Mating mayflies are further attracted to roads because of their elongated shape (much like a stream) and because there is no overhanging vegetation (a prerequisite for mating). This change in reproductive behaviour (mating and laying eggs on asphalt instead of water) is damaging to mayfly populations because eggs laid on asphalt perish (Kriska *et al.* 1998, Kriska *et al.* 2007). Most insects whose larvae develop in freshwater use polarotaxis to locate water sources (Kriska *et al.* 2009), including dragonflies (Odonata) and tabanid flies (Tabanidae), suggesting that many insects' reproductive behaviour can be interfered with by asphalt covered roads.

Roads are a source of ambient noise in the environment, with the level of noise pollution determined by the flow and weight of traffic. Noise acts as a strong deterrent to many species, keeping them away from the road vicinity. For example, some species of foraging bats will avoid areas with roads in favour of silent areas (Schaub *et al.* 2008). Light and noise pollution causes changes in animal foraging behaviour (Slabbekoon & Ripmeester 2008). Additional light can affect foraging behaviour, with bats that previously scanned for food over large areas now limiting their foraging area to well lit roads. A study by Santos *et al.* (2010) found that visually foraging wading birds increased foraging effort in artificially illuminated areas, and that waders that used a mixture of visual and tactile foraging favoured more effective visual foraging style in light polluted areas. These shifts in foraging behaviour increased prey intake rate by an average of 83 %, an obviously positive effect of light pollution. Noise pollution leads to some animals devoting more time than usual scanning for predators in areas of elevated noise, such as near a busy road. Chaffinches, *Fringilla coelebs*, were found to spend less time foraging during artificially increased noise levels (Quinn *et al.* 2006) in order to 'look' for predators because auditory stimuli detection is reduced.

Animals such as birds and amphibians use calls and songs to attract mates and stake territory (Bee & Swanson 2007). Traffic noise from roads interferes with these acoustic signals and has led to changes in singing behaviour. Birds have been shown to increase song amplitude (volume), known as the Lombard effect, to compete with traffic noise (Brumm 2004) both in the field and in experiments using white-noise. Examples of birds that the Lombard effect has been shown in include, zebra finches *Taeniopygia guttata* (Cynx *et al.* 1998), budgerigars *Melopsittacus undulatus* (Manabe *et al.* 1998), blue-throated hummingbirds *Lampornis clemenciae* (Pytte *et al.* 2003), Nightingales *Luscinia megarhychos* (Brumm 2004) and domestic fowl (chickens) *Gallus gallus* (Brumm *et al.* 2009). An alternative to changing call amplitude is to change call frequency (pitch). Birds will generally increase the frequency of their signalling to avoid masking by traffic (which is usually low frequency) (Slabbekoon & Ripmeester 2008, Halfwerk & Slabbekoon 2009, Parris & Schneider 2009). Finally, many species alter their temporal pattern of acoustic signalling to avoid masking and interference from other species' calls (Warren *et al.* 2006). Given this, a temporal shift in signing activity in bird species, competing with traffic, is not unexpected. Such a shift usually changes diurnal singing patterns to avoid peak traffic. One such example is the European robin, *Erithacus rubecula*, (Fuller *et al.* 2007) that has been found to sing nocturnally in areas of high traffic.

Acoustic behavioural responses have also been seen in monkeys and frogs. Brumm *et al.* (2004) played white-noise to common marmosets (*Callithrix jacchus*) and found that in addition to increasing amplitude they also increased the duration of calls (although not studied with traffic, a similar response can arguably be expected from marmosets near roads). However not all animals are capable of changing their behaviour to compensate for road presence. For instance, Tree frogs (*Hyla arborea*) are not able to adjust their call frequency or temporal structures in response to traffic-noise and are therefore unable to transmit information to each other, reducing reproductive success (Lengagne 2008).

Responses of animals to noise pollution from roads are an issue of increasing concern for conservation and animal behaviour biologists (Warren *et al.* 2006). Behavioural responses may be short-term phenotypically plastic responses, long-term phenotypically plastic responses (e.g. song learning) or may be evolutionary responses under natural selection

(Warren *et al.* 2006), thus roads are capable of driving evolution as well as of shaping the landscape.

3.4. Habitat structure

Roads alter the structure of the landscape and associated habitats (McGarigal *et al.* 2001, Saunders *et al.* 2002). As soon as a road is laid habitat is destroyed and the remaining habitat is fragmented, during road operation edge effects reduce the suitability/quality of habitats for interior species. In one study it was found that mean patch size and core habitat area declined by 40 % and 25 % (respectively) as a result of logging road development over 40 years (McGarigal *et al.* 2001). On the other hand, roads provide new habitats, for example bridges provide new nesting sites for birds (Forman 1998, Kociolek *et al.* 2011) and road verges form new succession sites (Forman *et al.* 2003), thus the age of a road influences the community structure present (Spooner & Smallbone 2009). Alternatively, road verges can be planted and maintained, altering the original local diversity and structure of plant communities. The specifics of how a road edge/verge is managed can modify the effect the road has on biodiversity. For example, roads that have trees within 20 meters have lower owl mortality than those with trees more than 20 meters away, and roads with perches (trees/shrubs/hedgerows) taller than two meters experience less owl mortality than those with perches shorter than two metres (Hernandez 1988, Orlowski 2008). Small scale habitat structure is also altered by road presence, such as lower leaf litter depth near road edges that is possibly due to increased exposure of edges to wind (Haskell 2000). Changes to habitat structure leads to many abiotic changes, for example microclimates, hydrology, erosion rates and biogeochemical cycles are altered as a result of landscape and habitat structure change.

3.5. Microclimate

The microclimate surrounding a road differs from the microclimate of the surrounding natural environment for two main reasons: (1) the road surface has a different albedo to the surrounding habitat; and (2) roads are exposed and they expose the edges of the surrounding habitat. These two factors combine and result in differing microclimatic dynamics depending on the road and what the surrounding habitat is. For instance a small, quiet road passing through low grassland is likely to have less effect on the microclimate than a large, busy road passing through dense forest. Roads typically have a lower albedo than natural habitats and so are generally warmer than surrounding areas. This is taken advantage of by basking reptiles (Vijayakumar *et al.* 2001) and birds that rest on road surfaces, reducing their metabolic costs (Kociolek *et al.* 2011). By creating exposed edges, the area immediately surrounding a road has a higher temperature than further away from a road (especially in forested habitats). However, edges are more exposed to wind (natural or generated by traffic) which can reduce edge temperatures. By altering exposure, roads also change light levels and humidity. Changes in soil moisture can be attributed to roads in several ways; changes in runoff rates as a result of the impervious nature of road surfaces increase moisture levels, while increased exposure along a road edge will result in drier soils. Roads do alter the microclimate but their effects are varied and depend on the changes and interactions between pre-existing habitat, road characteristics, and specific changes in exposure and light conditions.

3.6. Hydrology

Roads alter the hydrology of landscape in many ways, primarily through forming a hard, compacted surface that alters the flow of water run-off that can cause major changes in terrestrial (Young 1994) and aquatic systems (Forman & Alexander 1998, Jones *et al.* 2000, Coffin 2007). Changes in run-off regimes can lead to flooding, with roads increasing the amount of water reaching a stream system (Spellerberg 2002, Forman *et al.* 2003). Roads increase the peak flow of streams and rivers by increasing the amount and rate at which water is introduced via run-off (Jones *et al.* 2000). If the roads have a drainage system that connects to the waterways, then the road network extends the drainage basin of the stream system (Forman & Alexander 1998). Flowing water shapes landscapes via streams and rivers; roads generally result in more water runoff and consequently faster flowing water, faster flow is stronger flow and results in faster changes to the landscape. For example, over time river bends become deeper as the faster flowing water on the outside of the bend cuts into the land and the slower flowing water on the inside deposits sediment.

Faster water flow can alter more than just the shape of the waterway. Aquatic species are adapted to certain flow rates and regimes (Bain *et al.* 1988), and by altering these conditions roads can lead to changes in species composition of the waterway. Species that are adapted to survive in slow moving water may not be able to cope with the increase in flow rate as a result of increased run-off, so stream communities will move from slow water adapted species to those that can cope with increased flow. Also, faster flowing streams have reduced community complexity compared with slow flow stream systems (Bain *et al.* 1988).

Roads increase the natural instability of montane habitats (Young 1994), with an increased frequency of landslides observed in steep-forested landscapes with roads compared with equivalent landscapes with no roads (Jones *et al.* 2000). Increased run-off from roads results in more erosion (McGarigal *et al.* 2001) which, coupled with an increase in landslides, results in increases in the 'debris flow' of stream networks and thus higher deposition of sediment into waterways. Sediment clouds the water and thus changes suitability of the system for many aquatic species.

Increased run-off removes topsoil and reduces the fertility of areas in the run-off path, potentially reducing productivity. Increased runoff and associated erosion introduces an increased amount of chemical pollutants (heavy metals and nutrients), leached from the land, into coastal and inland aquatic systems, which inevitably has knock on effects in these systems (Davidson *et al.* 2010).

3.7. Pollution

The presence of a road is inevitably associated with vehicular traffic, which by its nature, introduces chemical and physical pollutants into the environment. Light, noise (discussed above), dust (particular pollutants), chemicals (de-icers and herbicides), metals (lead, nickel, zinc) and gases (carbon dioxide, sulphur, nitrous oxides, volatile organic compounds (VOC's), polycyclic aromatic hydrocarbons (PAH's) are all released into habitats surrounding roads (Bignal *et al.* 2007). Although most pollutants are introduced to the environment via combustion reactions in vehicles, pollutants may also come from road construction or the road surface itself, management regimes or from spillages (e.g. oil/petrol).

Some chemicals released into the atmosphere add to climate change and those that enter habitats alter the chemical composition of soil and waterways, potentially affecting the local fauna and flora. The range of chemical pollutants is large and there is a vast variation in the level of study dedicated to each; with some pollutants being comprehensively investigated (e.g. nitrous oxides) and others hardly studied at all (e.g. PAH's (Spellerberg 2002)).

Metals introduced to the environment by vehicle exhausts have been extensively studied (Spellerberg 2002), although little is known about the ecological impacts of most metal pollutants (Bingal *et al.* 2007). Lead (Pb) is one of the most extensively studied metal pollutants. Lead was previously used in petrol in order to increase octane number (Majdi & Persson 1989) and for 'anti-knock' properties (Storch *et al.* 2003). Although no longer used in most of the developed world, there are still developing regions where leaded petrol is still available and used as fuel. For example in Africa most petrol sold contains between 0.5-0.8 g/L of lead, far exceeding the WHO's guideline of 0.15 g/L (Ebenso & Ologhobo 2008). Lead negatively effects tree root tip growth, with Majdi & Persson (1989) showing that root tips per unit length decreased closer to roadsides, which inevitably negatively impacts the health of trees near roadsides. Snail shells have also been found to be thinner at lead polluted sites, and their tissue contains high levels of pollutants (including lead) which can be passed up the food chain (Ebenso & Ologhobo 2008). However, not all metal pollution has negative impacts, with calcium (Ca) levels increasing near roadsides that are paved with limestone leading to increases in the dry mass of snails and millipides with proximity to these roads because there is more 'acquirable' calcium that can be utilised in shell and exoskeleton growth (Kalisz & Powell 2003). That same calcium, however, can alter the pH of the surrounding soil using limestone or other base-rich materials in acidic areas leads to an increase in soil pH (Kalisz & Powell 2003, Spellerberg 2002). Conversely, introducing acid-rich material results in a pH decrease. A change in pH can be very detrimental to floral communities that are adapted to either basic or acidic environments (Spellerberg 2002).

'Dust' is a particular pollutant consisting of any solid matter that is fine enough to be raised and carried by wind (Farmer 1993). Depending on the material a road is built of, the type of dust raised will vary, with tarmac roads having the least dust and dirt roads the most. Dust may have chemical or physical impacts and the precise nature of these impacts will depend largely on the physical and chemical nature of the road material from where the dust originates. A review by Farmer (1993) found the presence of dust on a leaf surface may smother the leaf reducing photosynthesis. Dust can block stomatal openings and even stop gas exchange, inhibit pollen germination, halt starch production, stimulate leaf necrosis, reduce transpiration, reduce enzyme activity, and ultimately reduce fruit set and increase leaf temperature (which can disrupt biochemical processes).

Nitrogen pollution introduced in the forms of nitrous oxides from vehicle exhausts is beneficial to some plant species. Heather (*Calluna vulgaris*) and other grasses on heathland habitats close to roads experience increased growth in nitrogen polluted areas (Angold 1997). However heather is adapted to low nutrient, acidic soils (Iason & Hester 1993). When exposed to nitrogen pollution the abundance of heather decreases, despite improved individual growth rates. Grass species' abundance increases, leading to a shift in community composition, with heather and lichens declining and grasses increasing in abundance (Angold 1997). Nitrogen run-off into aquatic systems can lead to eutrophication and algal blooms.

Other pollutants from car exhausts include sulphur dioxide which, although beneficial at low concentrations, generally alters photosynthetic reactions and thereby reduces growth and productivity (Swanepoel *et al.* 2007). Particulate carbon can behave like a fertilizer and alter plant community composition (Bazzaz & Garbutt 1988, Hunt *et al.* 1991), and ethylene which is used in many plant processes including fruit ripening and leaf senescence, causes disruptions to normal plant phenology (Taiz & Zeiger 2006).

Road management regimes such as de-icing, herbicide and pesticide treatments introduce various pollutants into the environment. De-icers increase the salinity of roadside soil which has effects on the surrounding vegetation and, when transported in run-off, causes negative effects in more distant vegetation and aquatic systems. Increased salt can kill many plant species and increases the susceptibility of some tree species to fungal infections (Spellerberg 2002). De-icing regimes facilitate the dispersal of halophytic plant species, often shifting community dominance in favour of salt-loving or tolerating species. De-icers increase the salinity of local plant species which can be beneficial to herbivores for whom salt is a limited resource (Laurian *et al.* 2008) but ingestion of salts by birds can be fatal (Mineau & Brownlee 2005, Kociolek *et al.* 2011). Run-off transported de-icing salts cause decreases in weight and response times of frog larval stages (tadpoles) and in high concentrations cause developmental abnormalities and are fatal (Sanzo & Hecnar 2006). Herbicides and pesticides used to keep roads and lay-bys free from unwanted weeds and pests affect other plants and invertebrates in the vicinity and run-off into waterways.

3.8. Cumulative effects on ecological communities

Abiotic, individual and population level effects of roads have repercussions at a community level often affecting, species composition, abundance, community structure and diversity. Community composition is altered by roads through creating succession sites, altering microclimates and introducing alien species. Roads play a role in the spread of alien species including plants (Gelbard & Belnap 2003, Brisson *et al.* 2010), invertebrates (Suarez *et al.*

1998, Dong *et al.* 2008, Cameron & Bayne 2009) and vertebrates (Brown *et al.* 2006). Roads also play a role in the spread of pathogens, both native and alien (Jules *et al.* 2002, Urban 2006, Haemig *et al.* 2008). Invasions are facilitated by roads in a number of ways: (1) roads act as conduits/corridors for alien invasions, thus alien species are often more abundant near road edges (Spellerberg 2002, Watkins *et al.* 2003, Shepard *et al.* 2008,); (2) Roads lead to increased human activity; humans and their vehicles often carry invasive species with them over long distances (Jules *et al.* 2002); (3) Roads increase disturbances and disturbed habitats allow easier establishment of alien species (Hobbs & Huenneke 1992); (4) Road induced changes in abiotic conditions improve the suitability of road edges for alien species (Forman & Alexander 1998), with exposed road edges having higher light levels making edges suitable for aliens (Parendes & Jones 2000). The longer a road is active, the higher the chance of an alien introduction becomes because they are under a higher accumulated pressure of potential introductions than newer roads (Cameron & Bayne 2009). For example, six species of invasive earthworms in Canada are spread via road networks and older roads had a greater number and extent (i.e. are present further from the road boundary) of worms (Cameron & Bayne 2009).

Roads also have negative effects on community diversity, by increasing local extinction rates and/or decreasing recolonisation rates via, restricting movement, edge effects, changing abiotic conditions, introducing aliens and increasing human activity (Findley & Houlahan 1997). Vascular plant, invertebrate, amphibian, reptile and bird species richness has been found to be negatively impacted, and community structure altered, by roads (Findlay & Bourdages 2000, Haskell 2000, Watkins *et al.* 2003, Laurance 2004, Fahrig & Rytwinski 2009). However, the effect of roads on community diversity is subject to time lags and may not be evident for decades after road construction (Findlay & Bourdages 2000).

Changes in species abundance and richness can lead to knock on effects through food webs and species interactions. For example, soil macroinvertebrate abundance and richness is depressed near roads, predators that rely on soil invertebrates may face food shortages and thus population reductions. This is thought to be true for ground foraging birds like the Wood Thrush (*Hylocichla mustelina*), Black and white Warblers (*Mniotilta varia)*, and also woodland salamanders (Haskell 2000).

Very few generalisations can be made about the ecological effects of roads on biota; each species is likely to respond in a different way to the myriad of changes that roads bring about to the environment. One thing however may be said, overall, the effects of increasingly extensive road networks are negative. The Brazilian Amazon is a region undergoing widespread road network development. Although all of the discussed road effects may not be applicable to a tropical setting, the vast array of road effects that are applicable mean that it is very important that we understand where new roads are likely to emerge.

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