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From roadkill to road ecology: A review of the ecological effects of roads

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Abstract

Transportation infrastructure affects the structure of ecosystems, the dynamics of ecosystem function, and has direct effects on ecosystem components, including their species composition. Clearly, the construction of transport lines results in the direct destruction and removal of existing ecosystems, and the reconfiguration of local landforms. However, transportation systems, and more specifically, roads, have a wide variety of primary, or direct, ecological effects as well as secondary, or indirect, ecological effects on the landscapes that they penetrate. The effects of roads can be measured in both abiotic and biotic components of terrestrial and aquatic ecosystems. The nature of road systems as network structures renders vast areas of the landscape as road-affected, with small patches of isolated habitat remaining beyond the ecological influence of roads. The increasing attention of scientists to the unintended ecological effects of roads has resulted in the emergence of the science of ''Road Ecology,'' marked with the publication of a multi-authored volume, *Road Ecology: Science and Solutions*, in 2003.

Keywords: Road ecology; Road networks; Landscape ecology; Transportation and environment

1. Introduction

Transportation infrastructure is an artifact of culture that interacts with the surrounding landscape. Von Thünen's 1826 theory described how land use is a function, at least in part, of the cost of transport to markets (Wartenberg, 1966). Ullman (1956), in his contribution to *Man's Role in Changing the Face of the Earth* (1956), stated that ''Few forces have been more influential in modifying the earth than transportation.'' Transportation geographers have pointed out the correlation between transportation network expansion and economic development of regions (Kansky, 1963; Taaffe et al., 1963; Haggett, 1965). Roads, in particular, are physical manifestations of the social connections and the economic and political decisions that lead to land use change. The debate over whether landscape transformation is a cause or an effect of road network development belies the complexity of interactions between the social and biological realms which ultimately produce these networks. Their existence depends on social structures, and their physical characteristics depend partly on landscape structure.

The environmental effects of transportation systems are of interest to transportation geographers, but are relegated to the margins of the field, leaving room for exploration. Transportation geographers of the mid to late 20th century who examined the structure of transportation systems focused on their network properties, and their effects on land use, allocation, and competition between producers, manufacturers, distributors and consumers (Garrison et al., 1962; Beckman, 1967; Taaffe and Gauthier, 1973; Lowe and Moryadas, 1975). They produced a wealth of knowledge about the structure of transportation networks and derived a number of quantitative tools for their study (Haggett and Chorley, 1969). In this body of work, roadway systems were considered part of the required infrastructure for increasing productivity in a region, their physical structure a benign necessity in the promotion of

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progress. More recently, environmental topics have garnered more attention from transportation geographers, however, most of the discussion is focused on issues of sustainable transport and the quality of human life (Black, 1989; Gordon, 1991; Black, 1996; Hunter et al., 1998). Little attention has been given by geographers to the unintended consequences of road networks, or how their expansion affects the landscapes that they bisect. Far from being anonymously inert features, roads and their concomitant traffic introduce pollutants and exotic elements, fragment populations of plants and animals, kill animals and cause behavioral changes (Forman et al., 2003).

As early as the 1970s, wildlife biologists began publishing research on the effects of roads on wildlife populations as barriers to movement (Oxley et al., 1974; Wilkins, 1982; Mader, 1984; Mech et al., 1988; Brody and Pelton, 1989; Mader et al., 1990; Develey and Stouffer, 2001; Bhattacharya et al., 2003), sources of mortality (Bellis and Graves, 1971; Wilkins and Schmidly, 1980; Davies et al., 1987; Cristoffer, 1991; Groot Bruinderink and Hazebroek, 1996; Mumme et al., 2000; Main and Allen, 2002; Smith and Dodd, 2003; Dodd et al., 2004) and the cause of behavior modification (Rost and Bailey, 1979; Van Dyke et al., 1986; Brody and Pelton, 1989; Norling et al., 1992; Kerley et al., 2002; Tigas et al., 2002). Coincident with the development of landscape ecology and landscape scale analyses, attention has turned to the broader scale effects of landscape connectivity and habitat fragmentation, and, specifically, the effects of roads in fragmenting the landscape and interacting with landscape processes (Andrews, 1990; Reed et al., 1996; Canters et al., 1997; Strittholt and DellaSala, 2001; Heilman et al., 2002; Saunders et al., 2002; Bhattacharya et al., 2003; Hawbaker and Radeloff, 2004).

In recent years, interest in the ecological effects of roads on ecosystems and landscapes has increased, evidenced by a number of review papers published in scientific journals and edited volumes (Andrews, 1990; Bennett, 1991; Forman and Alexander, 1998; Spellerberg, 1998; Carr et al., 2002; Havlick, 2002; Trombulak and Frissell, 2002). With the clamor to review and consolidate information about the ecological effects of roads, research into this field is surging forward at the impetus of landscape ecologists and conservation biologists. One result of this attention has been to underscore the weaknesses of a landscape fragmentation "paradigm" which generally ignores anthropogenic causes such as land use intensification and urbanization (Laurance and Cochrane, 2001).

The term "road ecology" was coined by landscape ecologist Richard T.T. Forman in 1998 (Forman, 1998). It refers to an emerging subject of ecological investigation building on the mounting evidence that roads are having dramatic effects on ecosystem components, processes and structures, and that the causes of these effects are as much related to engineering as to land use planning and transportation policy. Road ecology is rooted in ecology, geography, engineering and planning. While research on the ecological effects of roads and transportation has been occurring in North America, Europe and Australia for some decades, the publication of the book *Road Ecology* (Forman et al., 2003), heralded the consolidation of this endeavor at a new conceptual scale, under the auspices of an interdisciplinary scientific umbrella.

The purpose of this paper is to present an overview of the literature describing the various ecological effects of roads and the development of road ecology as a body of scientific inquiry. The paper first gives a synopsis of the ecological effects of roads on the abiotic components of ecosystems including interactions with hydrologic systems, sediment erosion and deposition dynamics, environmental chemistry and ambient noise. The next section of the paper deals with the effects of roads on biota, from the direct effects of road related mortality, i.e. "roadkill", to population fragmentation and road avoidance behavior. This section also considers the fact that roads create habitat for many plants and animals. The final section of the paper attempts to address the more complex aspects of the cumulative ecological effects of roads on landscapes. The most obvious of these is the fragmentation of landscapes as roads bisect large patches of a contiguous land cover. In addition to the fragmentation of the landscape caused by roads, however, are the cumulative ecological effects of roads when considered as networked systems. Ecological road network theory suggests that these cumulative effects may be influenced by the design and function of the network structure. In this, transportation planners have an important role to play in being able to analyze and predict the potential ecological effects of alternative transport scenarios by using the tools that have already been developed by transportation geographers. Applying transportation geography theories and methods to research in road ecology could advance our understanding about the dynamic between road systems and landscapes and help lessen the negative ecological effects of roads on the environment.

2. The effects of roads on abiotic components of ecosystems

Roads affect the abiotic components of landscapes including the hydrology, the mechanics of sediment and debris transport, water and air chemistry, microclimate and levels of noise, wind, and light adjacent to roadsides. The extent and intensity of the effects vary with the position of the road relative to patterns of slope, prevailing winds and surrounding land cover (Forman and Alexander, 1998). Roads can increase the energy of stream systems, causing channel erosion and scouring on one hand; on the other hand, cut banks of roads near streams can cause sedimentation to occur. Either way, the presence of roads and related infrastructure has measurable effects on the morphology of stream and river channels which in turn affects the biota. Air and water pollution is one of the most often recognized environmental effects of roads. Toxic chemicals associated with air and water borne particulates cause diseases and increased mortality in humans, and indeed, this aspect of transportation has been the focus of intense scrutiny by government researchers, regulators and lawmakers for several decades. However, the broader ecological effects of chemical pollution due to road related transportation has been less well-studied, although it is clear that toxins enter and persist in the environment and interact with biota.

2.1. Changes to hydrology and water quality

The nature of the interaction of roads with aquatic systems depends on their location relative to the drainage network and the slope. Roads act as a source of water where water runs off the surface of the road. They can serve as sinks for water, where water accumulates on roads (this is far less significant). Roads can act as barriers to water flowing downhill, but can also speed the removal of water (Jones et al., 2000). At the landscape scale, road networks interact with stream networks, increasing the stream drainage density, the overall peak flow in the stream drainage, and the incidence of debris flows in the drainage basin (Jones et al., 2000). Roads extend the drainage network of the stream network when drainage swales along roads directly connect to stream networks (Forman and Alexander, 1998). Faster moving water enters the stream channels increasing the energy of the stream system, eroding channel banks, scouring the channel and can increase the likelihood of flooding downstream (Dunne and Leopold, 1978).

2.1.1. Erosion and sediment transport

Roads are often associated with land uses that can, in tandem, cause changes to erosion and deposition rates of sediments in stream channels. Logging roads and logging are notable because forestry is commonly the first broad-scale land use causing the whole-sale anthropogenic removal of vegetation and exposure of soil in a watershed. The likelihood of mass movement of earth is higher following logging and floodplains experience overbank deposition following logging events in watersheds (Johnson et al., 2002). The sediment pulses throughout the stream basin and results in changes to the morphology of streams, depositing in channels and creating shallower pools. The shallowness of the pools, combined with increased turbidity of the water and less vegetated banks, raises the temperature of the water in the streams. This stresses fish species that require colder temperatures, and favors other species that do not. Such a case was discovered in the Navarro watershed where logging practices and the associated roads created favorable conditions for the reproduction and growth of the common fish species California roach (*Lavinia symmetricus*), while stressing the steelhead trout (*Oncorhynchus mykiss*) and coho salmon (*Oncorhynchus kisutch*). In the North Fork basin of the Navarro watershed, 100% of the sediment eroded from cut banks along a highway in close proximity to the main stream channel was delivered to the channel network (Johnson et al., 2002).

2.1.2. Introduction of chemical pollutants

Sources of chemical pollutants along roadsides include the vehicles that use the road as well as the roads and bridges themselves, and the maintenance activities associated with the roadway. Chemical spills along roads are also an important source of chemical pollutants (US Environmental Protection Agency, 1996, 2001; Grant et al., 2003). Some chemicals affect only the areas nearest the road itself, while other chemicals are transported, via water or wind, greater distances from the road (Forman et al., 2003).

Toxic contaminants from roads enter the broader landscape most importantly via stormwater runoff. The contaminants in runoff vary greatly in size, over six orders of magnitude, and include hydrated ions, dissolved, colloidal and gravitoidal particles, and suspended matter. This makes the research and assessment of their ecological effects difficult, as a variety of tests must be used to analyze the different fractions of contaminants. Heavy metals and organic compounds are often adsorbed onto particles such as clay, silt and sand, associated with the road and roadbed. Many best management practices (BMPs) aimed at mitigating for chemical contaminants at the roadside are geared toward reducing the influx of particles into the surrounding landscape (Grant et al., 2003). The toxicity of contaminants depends on the way particulates affect organisms, such as altering the level of exposure to the toxin. The effectiveness of mitigation for chemical toxicity associated with roadway runoff depends on the extent to which contaminants associate themselves with particles that are removed by BMPs and the effectiveness of the BMPs (Grant et al., 2003).

A complex and wide array of contaminants associated with vehicles are introduced to the landscape via roadway runoff. Among them are hydrocarbons, asbestos, lead (Pb), cadmium (Cd), and copper (Cu). In addition, chemicals associated with the road itself or its maintenance, including pesticides, insecticides and deicing salts (e.g., magnesium chloride) combine with runoff and make their way into storm water drainage systems (US Environmental Protection Agency, 2001, 1996; Trombulak and Frissell, 2002; Grant et al., 2003).

Volatile chemicals associated with roads are introduced to the environment from vehicle emissions. These include carbon monoxide (CO), nitrogen oxides (NO_X), volatile organic compounds, sulfur dioxide (SO_2), particulates from exhaust and road dust, lead (Pb), methane (CH_4), and toxics including benzene, butadiene and formaldehyde. In addition to these primary emissions, some chemicals react to form secondary pollutants in the air. Chief among these is ozone, which is produced when nitrogen oxides combine with volatile organic compounds in the air. In the United States the emissions of chemicals increased rapidly until, in the 1970s and 1980s, pollution controls helped to reduce some emissions from vehicles, with lead emissions seeing the most dramatic declines in recent decades. Despite this decline, the estimated premature death in 1991 due to respiratory ailments caused by motor vehicle air pollution was equivalent to the number of deaths from motor vehicle accidents, approximately 40,000 (US Environmental Protection Agency, 1996). For this reason, air pollution is widely considered to be the most significant direct environmental effect of road related transportation. Air pollutants also enter aquatic systems and compound effects of stormwater runoff, with substantial inputs of nitrogen, metals and hydrocarbons to water bodies from atmospheric sources (US Environmental Protection Agency, 2001).

2.2. Noise and other atmospheric effects

Increased noise levels are one of the most significant environmental effects of highways, and are considered a nuisance to human populations in urban and suburban areas. In the United States, the Federal Highway Act of 1970 mandated the development of standards for noise and noise abatement relative to land use. Noise abatement studies are mandatory elements of the environmental impact assessment of highway construction projects. Mitigation for noise is a substantial part of the budget of any highway construction project and often results in the design and construction of specific noise abatement structures along highways (US Department of Transportation, 2000). Despite a several decades-long concern over the impact of highways on ambient noise levels, the effects of noise on populations of wildlife have not been as extensively researched. The Road Ecology Center at the University of California, Davis, recently sponsored a series of lectures in Road Ecology Center at the University of California (2005), to focus attention on the subject of the effects of noise on wildlife populations (2005), and a session of the 2005 International Conference on Ecology and Transportation (ICOET) also focused on this theme (West, 2006; Dooling et al., 2005).

Road noise has a variable effect on animals. The most significantly impacted by road noise are those species that incorporate sound into their basic behavior, such as birds. Much of the effect depends on the frequency to which the species in question is attuned. The effects of roads will disproportionately affect those species for whom the frequency of the road noise interferes with the frequency of their calls. For example, great tits (*Parus major*) in the city of Leiden, the Netherlands, were found to sing at higher pitches in noisier environments to overcome the problem of masking caused by low-frequency noises of the urban din (Slabbekoorn and Peet, 2003). In addition, the patterns of noise produced by traffic fluctuate in time. There may be a varying effect of road noise on animals as determined by time of day or season of the year, depending on the daily and life cycle patterns of that animal.

Aside from road related noise problems, other atmospheric effects are produced by the physical structure of roads. Roads affect patterns of wind direction and speed, temperature, relative humidity and insolation. Generally, roadsides are windier and more turbulent, hotter, dryer and sunnier (Forman et al., 2003). In addition, the air is dustier near roads, particularly near unpaved roads. Road dust affects vegetation by covering surfaces and affecting photosynthesis, respiration and transpiration thereby resulting in injury and decreased productivity (Farmer, 1993). Dust provides adsorption surfaces for volatile contaminants that are subsequently deposited either by dry or wet deposition, and causing phytotoxic pollutants to enter plant tissues, and causing respiratory ailments in animals and humans. These microclimatic changes can affect areas great distances from the road, changing the vegetation composition for some distance away from roads (Forman and Deblinger, 2000; Farmer, 1993).

3. The effects of roads on biotic components of ecosystems

Roads are agents of change that have both primary, or direct effects, as well as secondary, or indirect effects on the biota (Bennett, 1991). Roads affect animal and plant populations directly by entirely obliterating the ecosystems in their path. While for some species, the destruction of a small area for a roadbed may not be significant, for some species, particularly small animals with high levels of site fidelity, it can be ruinous. Populations of slow moving animals and those which regularly cross roads suffer in particular from the negative effects of increased mortality due to vehicle collisions. Roads also act as conduits introducing and facilitating the spread of exotic species. The indirect effects of roads include changes or impacts that result from increased contact with humans and human land use activities.

3.1. Roads as sources of mortality and barriers to animal movement

In the United States, roadkill has surpassed hunting in its effect on vertebrate mortality (Forman and Alexander, 1998). While some species with high roadkill rates (e.g. house sparrow, *Passer domesticus*) seem unaffected by the high rate of mortality associated with roads, others are much more affected, such as the Florida panther (*Felis concolor coryir*), which had an annual roadkill mortality rate of 10% of its population before 1991 (Forman and Alexander, 1998). In fact road related mortality is the primary source of mortality for all of Florida's "large, rare and endangered vertebrates," including panther, black bear (*Ursus americanus*), key deer (*Odocoileus virginianus clavium*) and American crocodile (*Corocodylus acutus*) (Harris and Scheck, 1991). This dubious distinction extends to the marine environment as well, with boat collisions being the largest known cause of mortality for the West Indian manatee (*Trichechus manatus latirostris*) in Florida's coastal waters (O'Shea et al., 1985; US Fish and Wildlife Service, 2001). While much of the focus on animal mortality has been on large mammals, herpetofauna are also significantly affected by roadkill. One of the most important mitigation projects in this regard is the "ecopassage" to alleviate roadkill rates on US. Highway 441 through Paynes Prairie State Preserve near Gainesville, Florida (Smith and Dodd, 2003; Dodd et al., 2004; Smith et al., 2005).

Harris and Scheck (1991) identified several reasons why roads and traffic are such significant sources of mortality for wildlife: migration routes and home ranges or territories are bisected by roads; animals intermingle with traffic as they move along open road corridors; new food resources, such as carrion and forage, are available in road corridors; and roadside environment is attractive and serves as an "ecological trap" or habitat for some species.

These observations suggest that the reasons that animals are killed by vehicles are driven mostly by the spatial arrangement of resources. Animals die when they are struck while trying to reach resources (food, water, den sites, etc.). Smith (1999, 2003) carried out an extensive spatial analysis of roadkill in Florida and suggested where planning and design efforts could mitigate vehicle-wildlife collisions taking into account the existing locations of roadkill, landscape patterns, animal distribution and movement patterns and questions of land and road ownership. Many researchers have also discovered a temporal pattern to roadkill that depends on varying resources, such as standing water during wet cycles, and life history, such as dispersal, hibernation or foraging patterns (Davies et al., 1987; Main and Allen, 2002; Saeki and Macdonald, 2004).

The direct mortality of animals due to vehicle collisions is a primary and obvious effect that reduces animal populations. In less populated areas, such as tropical forests, where traffic counts are low, animals may not risk being struck and killed by a vehicle. In these areas, increased human access corresponds with reduced densities of animals due in part to increased hunting pressure – a "secondary effect" of roads (Bennett, 1991; Robinson and Bodmer, 1999). This phenomenon is well understood in Amazonia where loggers access remote forests by paths, trails and rudimentary logging roads and, while logging in an area, trap and hunt game for local consumption or trade (Peres and Lake, 2003). This is one of the many secondary effects of logging (and logging roads) which also include land transformation as well as a number of socio-economic responses. It is thought that these cumulative secondary effects of logging may be more detrimental to the overall long-term health of tropical forests than the actual logging itself (Laurance, 2001). In the wake of loggers, poachers and local settlers also venture into the local forests and preserves to hunt for subsistence and to augment their incomes (Barnes et al., 1995; Altrichter and Boaglio, 2004). Thus the secondary effects of roads on wildlife mortality extend far beyond the road corridor per se.

With the pressure of increased mortality due to roadkill and hunting, many species have been observed to alter their behavior near roads or in areas where there are higher densities of roads. It has already been noted that birds are known to change their calls in response to the disturbance of road related noise. It also is apparent that some species learn how to avoid vehicle collisions with age. At 3 years old, the mortality rate for Florida scrub-jays (*Aphelocoma coerulescens*) living near roads is the same as birds living in non-roaded environments (Mumme et al., 2000). One possible explanation for this is that surviving jays learn to avoid automobiles. Other types of modification include adjusting behavior to avoid, spatially and temporally, human activities. Such is the case for bobcats and coyotes observed in urban environments (Tigas et al., 2002). For some species, the stress accompanied with road-related disturbance and behavioral changes can affect overall survivability. Amur tigers (*Panthera tigris altaica*) living in roadless areas stayed longer at kill sites, ate more meat, and ultimately survived longer than tigers living in areas with roads (Kerley et al., 2002).

That roads act as barriers which hinder the movement of animals and fragment breeding populations is one of the most often noted effects of roads. Every published review of the ecological effects of roads notes the importance of the barrier effect of roads. The extent of the effect is determined by the characteristics and behaviors of the species in question, the physical qualities of the road and road-related infrastructure, the characteristics of the road traffic, and the spatial configuration of the road relative to adjacent landscape. The phenomena of population fragmentation has been noted across taxon, affecting small mammals (Oxley et al., 1974), large mammals (Nellemann et al., 2001), understory birds (Develey and Stouffer, 2001), insects (Bhattacharya et al., 2003) and herpetofauna (Smith et al., 2005). It arises when populations of animals are subdivided into smaller groups and genetic exchange between the groups ceases to occur because the road is impassable. The overall effect is to make local extinctions more likely as sources of immigrants are disconnected (Johnson and Collinge, 2004).

3.2. Roads as habitat, corridor and conduit

Roads and road verges do provide habitat for some animals, particularly small mammals and insects (Oxley et al., 1974; Getz et al., 1978; Vermeulen, 1994; Brock and Kelt, 2004), and provide a source of food for carrion-feeders (Bennett, 1988). The use of roadsides by animals depends greatly on design and management of the verge (Forman and Alexander, 1998). Differences in mowing regimes or planting designs can vary the effect of roads on bird, insect and mammal populations.

In some cases, where the surrounding land cover has been extensively transformed, as in parts of Australia and The Netherlands, roadsides, or verges, are the only remnants of native vegetation remaining, and are important sources of biodiversity in the landscape (Hussey, 1999; Deckers et al., 2005). In these cases, the contribution of railway corridors is also very significant. Railway rights-of-way are often significant reserves of remnant native vegetation in landscapes that are predominantly agricultural. The benefits of remnant vegetation to animals depend on the width of the verge as well as the design characteristics of the roads. In the wheat belt of Western Australia, where the road verge is a significant portion of the remaining native vegetation, as the width of the verge increased the number of species in the verge increased (Arnold and Weeldenburg, 1990). The design characteristics of the road, including the width of the road, the height of the road above grade and the surface of the road determines the habitat characteristics for species that might use it thus. For example, kangaroo rats (*Dipodomys stephensi*) were more active in using dirt roads than gravel roads (Brock and Kelt, 2004). For some small mammals, road verges constitute a "long, ribbon-like habitat" along which they can move and disperse (Vermeulen, 1994).

Some large animals are known to use roads and the space above roads to move more easily through the landscape. Observations have discovered that these are wide ranging animals, using lightly-traveled roads and tracks. They include red fox (*Vulpes vulpes*), dingo (*Canis familiaris dingo*), wolf (*C. lupus*) cheetah (*Acinomix jubatus*) and lion (*Panthera leo*). Bats are known to use these spaces much as they would a gap in the forest. According to Bennett (1991) there are four types of movement patterns that utilize roadside habitat. These include: "local foraging movements; dispersal between separated populations; long distance migratory movements; and local or geographical range expansion." To the extent that roads can serve as conduits for movement, it is important to recognize that not all species can take advantage of the road space to forage, disperse or colonize. Many species, it has been noted, experience the road as an inhospitable environment and a barrier to movement.

The plants and animals that are facilitated by the road as a conduit for movement are often "generalist" species. These species are able to exploit highly variable ecological conditions, such as those found in roadside environments (Forman and Alexander, 1998). They are often very successful at using road verge to facilitate their persistence and spread across the landscape. For this reason, roads are often cited as major causal factors in the successful invasion of exotic flora and fauna (Gelbard and Belnap, 2003).

Many exotic plants, which fit into the generalist category, exist disproportionately in roadside corridors (Tyser and Worley, 1992; Watkins et al., 2003; Pauchard and Alaback, 2004). In addition to the non-native plants that are frequently used in roadside landscapes, non-native seeds and propagules are dispersed by vehicles and encounter environments in road verges where they can thrive (Schmidt, 1989; Lonsdale and Lane, 1994). Roadsides have abundant light, little competition for runoff water from established shrubs and trees, and are flushed with nutrients periodically as land is cleared adjacent to roads. The easy availability of limiting factors (i.e. light, water, nutrients), combined with aggressive dispersal mechanisms, repeated human introductions, and the high contiguity of roadsides that extend for hundreds of miles uninterrupted, make roadsides highly invasible spaces (Davis et al., 2000; Parendes and Jones, 2000; With, 2003).

This introduction and establishment process is illustrated well in the case of Cogon grass (*Imperata cylindrica*), which was first introduced to Florida in the 1940s and 1950s for purposes of forage and erosion control. While Cogon grass can disperse by seed, the seeds do not travel great distances. Dispersal by rhizomes is far more significant, and is particularly problematic when spread by road construction equipment, or by contaminated roadway fill. Following its intentional introduction in the 1960s, extensive road construction occurred in the regions where it was introduced. By the mid-1980s Cogon grass was considered a noxious weed along highway rights-of-way, with severe infestations in North Central Florida, near Gainesville, which was one of the points of introduction (Dean et al., 1989; Willard et al., 1990).

Red imported fire ants (*Solenopsis invicta*) followed a similar trajectory. Although it was accidentally introduced to Mobile, Alabama, in the 1930s this species spread quickly throughout the southeastern United States. It has since spread to the Florida Keys where it is threatening many rare and endangered endemic species. While fire ants are found in all habitat types, they were most often encountered within 150 m of a road or development (Forys et al., 2002).

4. Ecological effects of road networks

While roads have many direct ecological effects on adjacent aquatic and terrestrial systems, as network structures, they also have far reaching, cumulative effects on landscapes which have been less well-studied (Riitters and Wickham, 2003). Some major effects to landscapes that directly relate to roads include the loss of habitat through the transformation of existing land covers to roads and road-induced land use and land cover change (Angelsen and Kaimowitz, 1999); and reduced habitat quality by fragmentation and the loss of connectivity (Theobald et al., 1997; Carr et al., 2002). Together they point to the larger issue of the synergistic effects of roads and road networks on ecosystems at broader scales (Forman et al., 2003).

4.1. Landscape change and fragmentation

In tropical forested areas, econometric models of land use and land cover change have revealed important relationships between biophysical and economic variables relative to roads. Not surprisingly, in rural areas, particularly in developing countries, the presence of roads has been most strongly correlated with processes of land cover change by facilitating deforestation (Chomitz and Gray, 1996; Angelsen and Kaimowitz, 1999; Lambin et al., 2001; Mertens and Lambin, 1997). The impact of roads, however, is not uniform. The spatial model developed by Chomitz and Gray (1996) examining the effects of road building on deforestation in Belize shows a sensitivity to soil quality, land tenure regulations and market access. They concluded that these three factors ‘‘have strong interactive effects on the likelihood and type of cultivation’’ (Chomitz and Gray, 1996, p. 501). In an area such as Belize with a low-density population, farmers will not simply follow logging roads to establish farms on poor-quality land. The conversion of forest to agriculture is more likely to occur on lands that have higher quality soils and greater access to markets, and are not protected State Reserves.

Spatial models that take into account the effects of roads on deforestation processes have become much more common in recent years (Mertens and Lambin, 1997; Stone, 1998; Munroe et al., 2002). A recent study examined the process of deforestation by crossing spatial analysis studies with livestock economic studies to understand the processes of land cover change in the Brazilian Amazon (Mertens et al., 2002). In this case, road construction ‘‘unambiguously increases the incentives’’ to convert forests to other uses. However, the effect of road construction varies and depends on the type of road, the stage of economic development in the region and variably affects land owners according to their production status. The main roads that formed the ‘‘lines of penetration’’ conceived of by Taaffe et al. (1963), were more important in the early colonization process, where the recent forest clearing is more closely associated with the development of ‘‘feeder lines’’. In the Brazilian Amazonian case, the roads were more important in providing market access to small scale producers rather than large cattle ranchers, for whom the presence or absence of roads is less of a constraint. Therefore, the development of roads was more important in explaining deforestation processes in the case of colonization than in the case of large-scale cattle ranching.

As elicitors of landscape fragmentation, roads appear to have the upper hand over other anthropogenic causes. To the extent that the road network is extended and connected, the landscape becomes more fragmented and less well connected. Reed et al. (1996) found in the Rocky Mountains that roads created more forest fragmentation than clearcut logging by ‘‘dissecting large patches into smaller pieces.’’ In numerous studies, densities of species are correlated either with road density (negatively) or with distance from road (positively) (Barnes et al., 1995; Canaday, 1996; Huijser and Bergers, 2000; Develey and Stouffer, 2001; Mech et al., 1988). These tend to be species that require interior forest conditions, require extensive home ranges and are shy, or are hunted. What's more, there is a time lag between the time of road construction and the effect of species decline, which varies by taxon (Findlay and Bourdages, 2000).

Conversely, the quality of ‘‘roadlessness’’ may be a significant determinant of survivability for some species. In a regional analysis of Wyoming, Montana and Idaho, the overall regional habitat connectivity increases, as measured by four landscape metrics of area, configuration, isolation and contagion, when roadless areas were included along with conservation areas (Crist and Wilmer, 2002). Another study in Alaska gave similar results, with roadless areas contributing significantly to regional measures of habitat connectivity (Strittholt and DellaSala, 2001).

4.2. Road edges and the ‘‘road-effect zone’’

The fragmentation caused by roads is alternatively measured by the amount of edge created by them. In many studies devoted to effects of roads on landscapes, references to the fragmentation of landscapes and the creation of edges are often coupled and used complementarily to describe the processes of change (Laurance and Williamson, 2001; Hawbaker and Radeloff, 2004). Ecological edges occur naturally throughout the landscape. They create the spatial patterns that result from environmental heterogeneity and the interactions between and among organisms (Turner et al., 2001). Ecological transitions, or ecotones, can result from changing resource availability, such as the transition from a marsh to a forest, corresponding with changing hydrologic conditions. Alternatively, edges are created when an ecological disturbance, such as a fire, creates a localized opening, like a gap in a forest (Forman, 1995). In this case, increased light and nutrients coupled with decreased competition from other plants allows for the colonization and establishment of other plant species, creating a distinctive edge.

Road edges, however, apart from being entirely human-induced, are peculiar in their linear shapes, and are affected by the dynamics of transport economics, distinguishing them from other types of edges. Reed et al. (1996) found that the amount of edge created by roads was 1.54 to 1.98 times that created by clearcuts. While it is true that road edges provide resources for some species (Section 3.2), they are most often noted by ecologists for their far-reaching negative consequences to ecosystem structures and flows. The edge effect of roads variably extends several meters into the adjacent landscape and is responsible for rendering vast areas as uninhabitable to many others (Forman et al., 2003). The microclimatic changes produced by even narrow roads affect the leaf litter and vegetation composition, soil macroinvertebrates, interior-dwelling forest birds, herpetiles, mammals and overall species richness (Willard and Marr, 1971; Haskell, 2000; Godefroid and Koedam, 2004). In the Amazon, overall positive feedbacks have been noted between increasing fires and drought conditions, i.e. regional climate change, and the amount of forest fragmentation and deforestation, directly related to the construction of roads (Laurance and Williamson, 2001).

The strength of the ecological effects of roads on adjacent non-road areas is a variable phenomenon, changing both in space and time. This ‘‘road effect zone’’ is determined as the zone adjacent to roads where one or more direct ecological effects of the road can be discerned. The convoluted shape of the zone can extend laterally to cover areas many times greater than the dimension of the road and its verges, depending on the ecological process and sensitivity of the species in question (Forman et al., 1997). While the significance of this concept cannot be underestimated, measuring the road-effect zone is as yet complex and imprecise and the development of tools to assess the landscape scale effects of road edges is not yet well-developed (Ries et al., 2004). Despite the difficulty of precisely locating the road effect zone, it is clear that the area of land ecologically affected by roads is vast, by virtue of proximity alone. On a continental scale, Riitters and Wickham (2003) estimated that approximately 83% of the land area in the conterminous United States to be within slightly more than 1 km of any road, and only 3% of the area slightly more than 5 km away.

4.3. Ecological road network theory

Cumulatively, road-effects interact with each other when roads are considered as systems. Ecological road network theory, which is comprised of basic principles of land use, transportation, network theory and ecology, provides a framework to interpret the ecological effects of road networks. With this theory as a basis, an analysis of the effects of a road network in a terrestrial ecosystem suggests that they extend over large areas of the landscape, that long-distance effects can saturate a landscape even in moderately roaded areas, and that isolated patches of habitat are created by road-effect patterns (Forman et al., 2003).

At this early stage in the development of road network theory, measuring the cumulative ecological effects of roads is far from well-developed. Indices that have been proposed include measuring road density, road location (Forman et al., 1997) and, using empirical methods, measuring road-effect zones on wildlife populations (Carr et al., 2002). Landscape ecological researchers are also considering the use of various modeling approaches to examine the problems (Carr et al., 2002; Forman et al., 2003). It is clear that the development of robust quantitative methods to model, explain and predict the interactions between road network structures and landscapes are important directions for future research. As a start, Jaeger et al. (2005, 2006) have used simulation modeling to predict the effects of road configuration on animal population persistence. They concluded that the effect of a gridded vs. parallel road network configuration depends on the target species' behavior, i.e. to what degree that species avoids crossing roads, and the probability of it being killed if it does. "Bundling" traffic (locating roads in close proximity to each other) is beneficial to population persistence, and core habitat areas that are unfragmented should be protected from road construction. They also conclude that while their modeling studies are an important step in developing ecological road network theory, empirical analysis comparing the effects of different road network configurations should be done.

Clearly there is potential in this area for a collaborative effort between road ecologists and transportation geographers. Although transportation geographers were prolific in developing quantitative indices of transportation network structures in the 1960s, this work is only beginning to find its way into road ecology literature (Forman and Alexander, 1998; Forman et al., 2003), and the indices have yet to be tested in modeling landscape/road-network interactions.

5. Conclusion

Wildlife biologists, observing the effects of traffic on animal mortality were the first to point out ecological consequences of roads, and the concern over these effects has grown such that Forman and Alexander (Forman and Alexander, 1998) refer to them as the "sleeping giant of conservation ecology." Roads affect both the biotic and the abiotic components of landscapes by changing the dynamics of populations of plants and animals, altering flows of materials in the landscape, introducing exotic elements, and changing levels of available resources, such as water, light and nutrients. Historically, the field of transportation geography has concerned itself mostly with the economic and structural aspects of transportation and implications for land use change. However, transportation geographers are in a unique position to contribute to the emergence of the science of road ecology, as the wealth of knowledge already developed can provide both theoretical and analytic tools to study the landscape scale effects of road networks.

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