# Review of Ecological Effects of Roads on Terrestrial and Aquatic Communities

STEPHEN C. TROMBULAK* AND CHRISTOPHER A. FRISSELL†

*Department of Biology, Middlebury College, Middlebury, VT 05753, U.S.A., email trombulak@middlebury.edu
†Flathead Lake Biological Station, University of Montana, 311 Bio Station Lane, Polson, MT 59860-9659, U.S.A.

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**Abstract:** *Roads are a widespread and increasing feature of most landscapes. We reviewed the scientific literature on the ecological effects of roads and found support for the general conclusion that they are associated with negative effects on biotic integrity in both terrestrial and aquatic ecosystems. Roads of all kinds have seven general effects: mortality from road construction, mortality from collision with vehicles, modification of animal behavior, alteration of the physical environment, alteration of the chemical environment, spread of exotics, and increased use of areas by humans. Road construction kills sessile and slow-moving organisms, injures organisms adjacent to a road, and alters physical conditions beneath a road. Vehicle collisions affect the demography of many species, both vertebrates and invertebrates; mitigation measures to reduce roadkill have been only partly successful. Roads alter animal behavior by causing changes in home ranges, movement, reproductive success, escape response, and physiological state. Roads change soil density, temperature, soil water content, light levels, dust, surface waters, patterns of runoff, and sedimentation, as well as adding heavy metals (especially lead), salts, organic molecules, ozone, and nutrients to roadside environments. Roads promote the dispersal of exotic species by altering habitats, stressing native species, and providing movement corridors. Roads also promote increased hunting, fishing, passive harassment of animals, and landscape modifications. Not all species and ecosystems are equally affected by roads, but overall the presence of roads is highly correlated with changes in species composition, population sizes, and hydrologic and geomorphic processes that shape aquatic and riparian systems. More experimental research is needed to complement post-hoc correlative studies. Our review underscores the importance to conservation of avoiding construction of new roads in roadless or sparsely roaded areas and of removal or restoration of existing roads to benefit both terrestrial and aquatic biota.*

Revisión de los Efectos de Carreteras en Comunidades Terrestres y Acuáticas

**Resumen:** *Las carreteras son una característica predominante y en incremento de la mayoría de los paisajes. Revisamos la literatura científica sobre los efectos ecológicos de las carreteras y encontramos sustento para la conclusión general de que las carreteras están asociadas con efectos negativos en la integridad biótica tanto de ecosistemas terrestres como acuáticos. Las carreteras de cualquier tipo ocasionan siete efectos generales: mortalidad ocasionada por la construcción de la carretera; mortalidad debida a la colisión con vehículos; modificaciones en la conducta animal; alteración del ambiente físico; alteración del ambiente químico; dispersión de especies exóticas e incremento en el uso de áreas por humanos. La construcción de carreteras elimina a organismos sésiles y a organismos de lento movimiento, lesiona a organismos adyacentes a la carretera y altera las condiciones físicas debajo ella misma. Las colisiones con vehículos afectan la demografía de muchas especies tanto de vertebrados como invertebrados; las medidas de mitigación para reducir la pérdida de animales por colisiones con vehículos han sido exitosas solo de manera parcial. Las carreteras alteran la conducta animal al ocasionar cambios en el rango de hogar, movimientos, éxito reproductivo, respuesta de escape y estado fisiológico. Las carreteras cambian la densidad del suelo, temperatura, contenido de agua en el suelo, niveles de luz, polvo, aguas superficiales, patrones de escurrimiento y sedimentación, además de agregar metales pesados (especialmente plomo), sales, moléculas orgánicas, ozono y mutrientes a los ambientes que atraviesan. Las carreteras promueven la dispersión de especies exóticas al alterar los hábi-*

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*tats, al estresar a las especies nativas y proveer corredores para movimiento. Las carreteras también promueven el incremento de la caza y la pesca, el hostigamiento pasivo de animales y modificaciones del paisaje. No todas las especies ni todos los ecosistemas son afectados por las carreteras de igual forma, pero en general la presencia de carreteras está altamente correlacionada con cambios en la composición de especies, los tamaños poblacionales y los procesos hidrológicos y geomorfológicos que afectan a la estructura de sistemas acuáticos y reparios. Se necesita más investigación experimental para complementar estudios correlativos post-hoc. Nuestra revisión hace énfasis en que en trabajos de conservación es importante evitar la construcción de nuevas carreteras en áreas carentes de ellas o en áreas con pocas carreteras, además de remover o restaurar carreteras existentes con la finalidad de beneficiar tanto a la biota acuática como la terrestre.*

## Introduction

Among the most widespread forms of modification of the natural landscape during the past century has been the construction and maintenance of roads (Diamondback 1990; Bennett 1991; Noss & Cooperrider 1994). As conservation biologists seek to understand the forces that influence the viability of populations and the overall health of ecosystems, it is important that we understand the scope of the ecological effects of roads of all types, especially important as conservation biologists are asked to participate in the development and implementation of strategies to protect or restore elements of biological diversity and integrity.

Roads of all kinds affect terrestrial and aquatic ecosystems in seven general ways: (1) increased mortality from road construction, (2) increased mortality from collision with vehicles, (3) modification of animal behavior, (4) alteration of the physical environment, (5) alteration of the chemical environment, (6) spread of exotic species, and (7) increased alteration and use of habitats by humans. These general effects overlap somewhat. In some cases animals modify their behavior and avoid roads because of concentrated human activity along roads. Roads may facilitate the spread of invasive species by disrupting native communities and changing physical habitats. Roads may fragment populations through roadkill and road avoidance. Despite the difficulty of categorizing discretely the causal basis in every example, these seven categories provide a useful framework for assessing what is known and unknown about the ecological effects of roads.

Selective road removal, relocation, or remediation may provide ecological benefits in certain situations. Yet, although roads are commonly identified as important correlates or indicators of loss of ecological health (e.g., Noss & Cooperrider 1994), the specific mechanisms by which biota are affected are often complicated or uncertain. Therefore, mitigation or treatment of specific effects, whether during road design or in post-construction remediation, can be costly and fraught with uncertainty.

## Mortality from Road Construction

Road construction kills any sessile or slow-moving organism in the path of the road. The extent to which road construction contributes to direct mortality has not been estimated as has direct mortality from other forms of habitat destruction (e.g., Petranka et al. 1993). The fact that road construction kills individual organisms is obvious, however. The magnitude of such construction is not trivial; the 13,107,812 km of road lanes of all types in the conterminous United States, with an average width of 3.65 m per lane, have destroyed at least 4,784,351 ha of land and water bodies that formerly supported plants, animals, and other organisms (U.S. Department of Transportation 1996). The actual number is likely much higher because this estimate does not include shoulder pavement and land peripheral to the roadbed that is cleared during construction.

Construction may physically injure organisms adjacent to the path of construction. Roads built for extraction of white fir result in damage to trees that is visible up to 30 m from the road (Trafela 1987). Such damage contributes to a decline of up to 30% in forest productivity per rotation, due in part to a decline in growth of damaged trees. Construction also alters the physical conditions of the soil underneath and adjacent to the road. Riley (1984) showed that road construction increases soil compaction up to 200 times relative to undisturbed sites. These changes likely decrease the survival of soil biota that are not killed directly. Direct transfer of sediment and other material to streams and other water bodies at road crossings is an inevitable consequence of road construction (Richardson et al. 1975; Seyedbagheri 1996). High concentrations of suspended sediment may directly kill aquatic organisms and impair aquatic productivity (Newcombe & Jensen 1996).

## Mortality from Collision with Vehicles

Mortality of animals from collision with vehicles is well documented. Many reviews of the taxonomic breadth of the victims of vehicle collision have been published (e.g., Groot Bruinderink & Hazebroek 1996). Few if any terrestrial species of animal are immune. Large mammals ranging in size from moose (*Alces alces*) to armadillos (*Dasypus novemcinctus*) are the best-documented roadkills, probably due to interest in their demography and to their size (Bellis & Graves 1971; Puglisi et al. 1974;

Reilly & Green 1974; Holroyd 1979; Wilkins & Schmidly 1980; Bashore et al. 1985; Davies et al. 1987; Bangs et al. 1989; Palomares & Delibes 1992).

Roadkill among many other species includes American Kestrels (*Falco sparverius*; Varland et al. 1993), Barn Owls (*Tyto alba*; Newton et al. 1991), Northern Saw-whet Owls and Eastern Screech Owls (*Aegolius acadicus and Otis asio*; Loos & Kerlinger 1993), tropical forest birds (Novelli et al. 1988), garter snakes (Dalrymple & Reichenbach 1984), granivorous birds (Dhindsa et al. 1988), American crocodile (*Crocodylus acutus*; Kushlan 1988), green iguanas (*Iguana iguana*; Rodda 1990), desert snakes (Rosen & Lowe 1994), toads (van Gelder 1973), plus a wide range of invertebrates, especially insects (H. C. Seibert & Conover 1991).

This form of mortality can have substantial effects on a population's demography. Vehicle collision is the primary cause of death for moose in the Kenai National Wildlife Refuge in Alaska (Bangs et al. 1989) and for Barn Owls in the United Kingdom (Newton et al. 1991), the second highest form of mortality for Iberian lynx (*Felis pardina*) in southwestern Spain (after hunting; Ferreras et al. 1992), and the third highest form for white-tailed deer (*Odocoileus virginianus*) in New York (Sarbello & Jackson 1985) and wolves (*Canis lupus*) in Minnesota (Fuller 1989). Roadkill is a limiting factor in the recovery of the endangered American crocodile in southern Florida (Kushlan 1988) and is contributing to the endangerment of the prairie garter snake (*Thamnophis radix radix*; Dalrymple & Reichenbach 1984). Roadkill is often nonspecific with respect to age, sex, and condition of the individual animal (e.g., Bangs et al. 1989).

Amphibians may be especially vulnerable to roadkill because their life histories often involve migration between wetland and upland habitats, and individuals are inconspicuous and sometimes slow-moving. Roads can be demographic barriers that cause habitat and population fragmentation (Joly & Morand 1997). In the Netherlands, for example, roads with high traffic volume negatively affect occupancy of ponds by moor frogs (*Rana arvilis*; Vos & Chardon 1998). In Ontario, the local abundance of toads and frogs is inversely related to traffic density on adjacent roads, but the incidence of roadkill relative to abundance is higher on highly trafficked roads (Fahrig et al. 1995). Thus, even though populations in high-traffic areas have apparently already been depressed from cumulative road mortality, they continue to suffer higher proportionate rates of roadkill.

Mitigation measures have been employed in different locations with varying degrees of success (e.g., Yanes et al. 1995). For example, underpasses on Interstate 75 have been only partially successful in reducing roadkill of Florida panthers (*Felis concolor coryi*; Foster & Humphrey 1991). Despite mitigation efforts, roads are likely to be a persistent source of mortality for many species. In general, mortality increases with traffic volume (e.g., Rosen & Lowe 1994; Fahrig et al. 1995). Some species are less likely to be killed on high-speed roads than on medium-speed roads because the former usually have vegetation cleared back further from the road's shoulder, creating less attractive habitat and greater visibility for both animals and drivers. Other species, however, are attracted to the modified habitat alongside and in the meridians of high-speed roads (Cowardin et al. 1985), making them population sinks.

## Modification of Animal Behavior

The presence of a road may modify an animal's behavior either positively or negatively. This can occur through five mechanisms: home range shifts, altered movement patterns, altered reproductive success, altered escape response, and altered physiological state.

Black bears (*Ursus americanus*) in North Carolina shift their home ranges away from areas with high road densities (Brody & Pelton 1989), as do grizzly bears in the Rocky Mountains (*Ursus horribilis*; McLellan & Shackleton 1988). Elk (*Cervus elaphus*) in Montana prefer spring feeding sites away from visible roads (Grover & Thompson 1986), and both elk and mule deer (*Odocoileus hemionus*) in Colorado in winter prefer areas >200 m from roads (Rost & Bailey 1979). Wolves will not establish themselves in areas with road densities greater than a region-specific critical threshold (Jensen et al. 1986; Thurber et al. 1994), probably as a result of a relationship between road density and hunting pressure. Mountain lion (*Felis concolor*) home ranges are situated in areas with lower densities of improved dirt roads and hard-surface roads (Van Dyke et al. 1986), suggesting that either mountain lions avoid these areas or road construction tends to avoid their prime habitat. Elephants (*Loxodonta africana*) in northeastern Gabon preferentially locate in forests away from both roads and villages (Barnes et al. 1991). Both Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*), on the other hand, preferentially establish home ranges in areas with greater road densities (Coleman & Fraser 1989), probably because of the increase in carrion.

Roads may also alter patterns of animal movement. Caribou (*Rangifer tarandus*) in Alaska preferentially travel along cleared winter roads that lead in the direction of their migration (Banfield 1974). Although the road may enhance caribou movement, it results in increased mortality from vehicle collisions and predation by wolves. After calving, female caribou with calves avoid roads (Klein 1991). The land snail *Arianta arbustorum* avoids crossing roads, even those that are unpaved and as narrow as 3 m (Baur & Baur 1990), and extend their movements along road verges. Reluctance to cross roads is also seen in white-footed mice (*Peromyscus* *leucopus*; Merriam et al. 1989) and many other rodent species (Oxley et al. 1974), even when the road is narrow and covered only with gravel. Cotton rats (*Sigmodon hispidus*) and prairie voles (*Microtus ochrogaster*) avoid roads as narrow as 3 m (Swihart & Slade 1984). Black bear almost never cross interstate highways in North Carolina (Brody & Pelton 1989) but will cross roads with less traffic volume. Roads act as barriers to gene flow in the common frog (*Rana temporaria*) in Germany, leading to significant genetic differentiation among populations (Reh & Seitz 1990). Other animals that show a reluctance to cross roads include pronghorn antelope (*Antilocapra americana*; Bruns 1977) and mountain lions (Van Dyke et al. 1986).

Some animals seem unaffected by the presence of roads, at least at some spatial scales. Based on a study of 20 wolverines, Hornocker and Hash (1981) concluded that the sizes and shapes of home ranges of wolverines where they are still found in northwestern Montana are independent of the presence of highways. Similarly, the presence of highways explained none of the allelic differentiation among populations of brown hares (*Lepus europaeus*) in Austria (Hartl et al. 1989).

Roads may affect an animal's reproductive success. Productivity of Bald Eagles (*Haliaeetus leucocephalus*) in Oregon (Anthony & Isaacs 1989) and Illinois (Paruk 1987) declines with proximity to roads, and they preferentially nest away from roads. Golden Eagles (*Aquila chrysaetos*) also prefer to nest away from human disturbances, including roads (Fernandez 1993). The reduced nesting success of eagles in proximity to roads may be more a function of the presence of humans than of the road itself; nesting failure by Golden Eagles in Scotland correlates with how easy it is for people to approach but not with proximity to roads themselves (Watson and Dennis 1992). Relative to habitat availability, Sandhill Cranes (*Grus canadensis*) avoid nesting near paved and gravel public roads (Norling et al. 1992); they do not avoid private roads with low-traffic volume (Norling et al. 1992) and can habituate to roads over time (Dwyer & Tanner 1992). Mallards (*Anas platyrhynchos*) in North Dakota, on the other hand, prefer road rights-of-way for nesting (Cowardin et al. 1985), perhaps because of a lower level of predation there.

Roads can also alter escape responses. Pink-footed Geese (*Anser brachyrhynchus*) in Denmark are more easily disturbed when feeding near roads, flying away when humans approach within 500 m, a greater distance than when feeding in areas without roads (Madsen 1985). Both the Lapwing (*Vanellus vanellus*) and Black-tailed Godwit (*Limosa limosa*) are more easily disturbed near roads and have disturbance distances of 480–2000 m depending on traffic volume (Van der Zande et al. 1980). Less well known is the effect of roads and vehicles on an animal's physiological state. MacArthur et al. (1979) showed that heart rate and therefore metabolic rate and energy expenditure of female bighorn sheep (*Ovis canadensis*) increase near a road independent of any use of the road. Roads contribute to fragmentation of populations through both increased mortality and modification of behavior that makes animals less likely to cross roads. Fragmentation may be accelerated by roads when spatially critical habitat patches (e.g., "stepping stones") become unoccupied as a result of increased local mortality or reduced recolonization.

## Disruption of the Physical Environment

A road transforms the physical conditions on and adjacent to it, creating edge effects with consequences that extend beyond the time of the road's construction. At least eight physical characteristics of the environment are altered by roads: soil density, temperature, soil water content, light, dust, surface-water flow, pattern of runoff, and sedimentation.

Long-term use of roads leads to soil compaction that persists even after use is discontinued. Soil density on closed forest roads continues to increase, particularly during winter months (Helvey & Kochenderfer 1990). Increased soil density can persist for decades: logging skid trails in northeastern California over 40 years old have soil that is 20% more compacted than soil in nearby areas that have not been used as trails (Vora 1988).

The reduction of water vapor transport on a road with a hard surface increases the surface temperature of a road compared to bare soil, an effect that increases with thickness of the road surface (Asaeda & Ca 1993). The heat stored on the road surface is released into the atmosphere at night, creating heat islands around roads. Animals respond to these heat islands: small birds (Whitford 1985) and snakes, for example, preferentially aggregate on or near warm roads, increasing their risk of being hit by cars and, at their northern range limits, reducing energetic demands for breeding.

During the dry season, the moisture content of soils under roads declines even if the roads are not in use (Helvey & Kochenderfer 1990), probably in response to changes in soil porosity. Roads through forests also increase the amount of light incident on the forest floor. The amount of increase depends on how much of the original canopy and lower strata remain, which depends in turn on the width of the road and roadside verge. The increase in light increases the density of species that preferentially grow where light levels are high, such as early-successional, disturbance-adapted species such as the North American orchid *Isotria medeoloides* (Mehrhoff 1989).

Road traffic mobilizes and spreads dust, which when settled on plants can block photosynthesis, respiration, and transpiration and can cause physical injuries to plants (Farmer 1993). These effects are sufficient to alter plant community structure, especially in communities dominated by lichens and mosses (Auerbach et al. 1997). Although most sediment enters water bodies through overland flow or mass failure, dust from highly trafficked roads can serve as a source of fine sediments, nutrients, and contaminants to aquatic ecosystems (Gjessing et al. 1984).

Roads and bridges can alter the development of shorelines, stream channels, floodplains, and wetlands. Because of the energy associated with moving water, physical effects often propagate long distances from the site of a direct road incursion (Richardson et al. 1975). Alteration of hydrodynamics and sediment deposition can result in changes in channels or shorelines many kilometers away, both down- and up-gradient of the road crossing. The nature of such responses to channel and shoreline alteration is not always predictable; it may depend on the sequence of flood and sedimentation events after the alteration is made. Roads on floodplains can redirect water, sediment, and nutrients between streams and wetlands and their riparian ecosystems, to the detriment of water quality and ecosystem health. Roads are among the many human endeavors that impair natural habitat development and woody debris dynamics in forested floodplain rivers (Piégay & Landon 1997).

Road crossings commonly act as barriers to the movement of fishes and other aquatic animals (Furniss et al. 1991). Although many headwater populations of salmonid fishes are naturally migratory, they often persist today as fragmented headwater isolates, largely because of migration barriers created by road crossings and other human developments that fail to provide for fish passage (Kershner et al. 1997; Rieman et al. 1997). Salmonids and other riverine fishes actively move into seasonal floodplain wetlands and small valley-floor tributaries to escape the stresses of main-channel flood flows (Copp 1989), but valley-bottom roads can destroy or block access to these seasonally important habitats (Brown & Hartman 1988). Persistent barriers may encourage local selection for behaviors that do not include natural migration patterns, potentially reducing both the distribution and productivity of a population.

Roads directly change the hydrology of slopes and stream channels, resulting in alteration of surface-water habitats that are often detrimental to native biota. Roads intercept shallow groundwater flow paths, diverting the water along the roadway and routing it efficiently to surface-water systems at stream crossings (Megahan 1972; Wemple et al. 1996). This can cause or contribute to changes in the timing and routing of runoff (King & Tennyson 1984; Jones & Grant 1996; Ziemer & Lisle 1998), the effects of which may be more evident in smaller streams than in larger rivers (Jones & Grant 1996). Hydrologic effects are likely to persist for as long as the road remains a physical feature altering flow routing—often long after abandonment and revegetation of the road surface. By altering surface or subsurface flow, roads can destroy and create wetland habitats.

Changes in the routing of shallow groundwater and surface flow may cause unusually high concentrations of runoff on hillslopes that can trigger erosion through channel downcutting, new gully or channel head initiation, or slumping and debris flows (Megahan 1972; Richardson et al. 1975; Wemple et al. 1996; Seyedbagheri 1996). Once such processes occur, they can adversely affect fishes and other biota far downstream for long periods of time (Hagans et al. 1986; Hicks et al. 1991). Roads have been responsible for the majority of hillslope failures and gully erosion in most steep, forested landscapes subject to logging activity (Furniss et al. 1991; Hagans et al. 1986). Because most of these more catastrophic responses are triggered by the response of roads during infrequent, intense storm events, lag times of many years or decades pass before the full effects of road construction are realized.

Chronic effects also occur, however. The surfaces of unpaved roads can route fine sediments to streams, lakes, and wetlands, increasing the turbidity of the waters (Reid & Dunne 1984), reducing productivity and survival or growth of fishes (Newcombe & Jensen 1996), and otherwise impairing fishing (Buck 1956). Existing problem roads can be remediated to reduce future erosion potential (e.g., Weaver et al. 1987; Harr & Nichols 1993). The consequences of past sediment delivery are long-lasting and cumulative, however, and cannot be effectively mitigated (Hagans et al. 1986).

## Alteration of the Chemical Environment

More has been written about the effects of roads on the chemical environment than on all other effects combined. Maintenance and use of roads contribute at least five different general classes of chemicals to the environment: heavy metals, salt, organic molecules, ozone, and nutrients.

A variety of heavy metals derived from gasoline additives and road deicing salts are put into the roadside environment. The most widely documented is lead, but others include aluminum, iron, cadmium, copper, manganese, titanium, nickel, zinc, and boron (Garcia-Miragaya et al. 1981; Clift et al. 1983; Gjessing et al. 1984; Oberts 1986; Araratyan & Zakharyan 1988).

Heavy metal contamination exhibits five patterns. First, the amount of contamination is related to vehicular traffic (Goldsmith et al. 1976; Dale & Freedman 1982; Leharne et al. 1992). Second, contamination of soils, plants, and animals decreases exponentially away from the road (Quarles et al. 1974; Dale & Freedman 1982). Most studies indicate that contamination declines within 20 m but that elevated levels of heavy metals often occur 200 m or more from the road. The pattern of decline is influenced by prevailing wind patterns (Haqus & Hameed 1986). Once metals reach aquatic environments, transport rates and distances increase substantially (Gjessing et al. 1984).

Third, heavy metals can be localized in the soil, either close to the surface if downward transport has not occurred (Indu & Choudhri 1991) or deep below the surface if pollution levels in the past exceeded those in the present (Byrd et al. 1983). Transportation and localization is largely affected by the physical properties of the soil (Yassoglou et al. 1987). Metals and other persistent chemicals fixed to soils may become remobilized once they are inundated or transported to freshwater environments by wind, water, or gravity.

Fourth, heavy metals accumulate in the tissues of plants (Datta & Ghosh 1985; Beslaneev & Kuchmazokova 1991) and animals (Collins 1984; Birdsall et al. 1986; Grue et al. 1986). As with soil, contamination of plant tissue occurs up to at least 200 m from a road and is greatest for individuals along roads with high traffic volume.

Fifth, heavy metal concentrations in soil decline over time where use of leaded gasoline has been stopped and surface-water flow carries the metal ions away (Byrd et al. 1983; Tong 1990). After they leave the terrestrial environment, however, the mobilized metals may cause additional harm to aquatic biota. Also, some of the processes of metal demobilization may be reversed rapidly if environmental conditions, such as acidity of the soils, sediments, or water, change (Nelson et al. 1991).

Deicing salts, particularly NaCl but also $CaCl_2$, KCl, and $MgCl_2$, contribute ions to the soil, altering pH and the soil's chemical composition (Bogemans et al. 1989). As with lead, discontinuation of the use of deicing salts allows plants damaged by salt stress to recover (Leh 1990). The effects on aquatic biota of temporary surges of salt that often accompany runoff from roads to surface and groundwaters have received little study. Deicing salts on roadways elevate chloride and sodium concentrations in streams (Molles & Gosz 1980; Hoffman et al. 1981; Peters & Turk 1981; Mattson & Godfrey 1994) and in bogs, where road salts can alter patterns of succession in aquatic vegetation (Wilcox 1986). Accumulation of salts from chemicals used for road deicing or dust control can disrupt natural stratification patterns and thus potentially upset the ecological dynamics of meromictic lakes (Hoffman et al. 1981; Kjensmo 1997).

Organic pollutants such as dioxins and polychlorinated biphenyls are present in higher concentrations along roads (Benfenati et al. 1992). Hydrocarbons may accumulate in aquatic ecosystems near roads (Gjessing et al. 1984). In one stream along a British highway, numerous contaminants were present at elevated levels in the water column and sediments, including copper, zinc, and various hydrocarbons, but polycyclic aromatic hydrocarbons associated with stream sediments accounted for most of the observed toxicity to aquatic amphipods (Maltby et al. 1995). Comparatively little research has focused on the questions of the fate and effects of the organic chemicals associated with roads.

Vehicles produce ozone, which increases the concentration of this harmful molecule in the air, especially in areas where vehicle exhaust accumulates (Flueckiger et al. 1984). Roads are also especially important vectors of nutrients and other materials to aquatic ecosystems, because the buffering role normally played by riparian vegetation (Correll et al. 1992) is circumvented through direct runoff of materials in water and sediment where roads abut or cross water bodies. Water moving on and alongside roadways can be charged with high levels of dissolved nitrogen in various forms, and sediment brings a phosphorus subsidy when it reaches surface waters. Road deicing salts are an additional source of phosphorus (Oberts 1986). The degree to which roads directly contribute to eutrophication problems in aquatic ecosystems has been little investigated. Because roads deliver nutrients that originate in the contributing slope area, the nutrient burden is probably largely controlled by surrounding vegetation and land use. An increased density of road crossings of water bodies can be expected to increase delivery of nutrients.

The alteration of the chemical environment by roads results in a number of consequences for living organisms. First, in the terrestrial environment the chemical composition of some woody plants changes in response to pollution. These changes include increased concentrations of chemicals produced by plants, such as terpenoids, which help them resist the toxic effects of pollution (Akimov et al. 1989) and salts (Bogemans et al. 1989), and decreased production of other chemicals, such as soluble protein and chlorophyll *a*, which are necessary for plant function (Banerjee et al. 1983).

Second, organisms may be killed or otherwise displaced as a result of chemical exposure. Virtually all measures of soil biotic diversity and function decline in contaminated soil, including abundance, number of species, species composition, index of species diversity, index of equability, and bulk soil respiration (Muskett & Jones 1981; Guntner & Wilke 1983; Krzysztofiak 1991).

Third, the growth (Petersen et al. 1982) and overall physical health (Flueckiger et al. 1984; Moritz & Breitenstein 1985) of many plants is depressed, even to the point of death (Fleck et al. 1988). The sensitivity of plants to pollutants may change during development; for example, seedlings are more sensitive to salt than are adults (Liem et al. 1984), which influences juvenile recruitment. Pollutants may affect plant health by damaging fine roots, mycorrhizae (Majdi & Persson 1989), and leaves (Simini & Leone 1986) and by changing salt concentrations in plant tissues (Northover 1987). Secondary effects on plant health include decreased resistance to pathogens (Northover 1987), causing further declines. In aquatic environments, plant (and animal) assemblages may change due to direct and indirect responses to nutrient increases and due to growth suppression or mortality caused by other chemicals introduced by roads.

Fourth, plants (Graham & Kalman 1974; Nasralla & Ali 1985; Dickinson et al. 1987; Guttormsen 1993) and animals (Robel et al. 1981; Collins 1984; Harrison & Dyer 1984; Krzysztofiak 1991; Marino et al. 1992), including those cultivated or raised for agriculture, may accumulate toxins at levels that pose health hazards, including those for humans that consume exposed organisms (Jarosz 1994).

Fifth, increased concentrations near roadsides of some pollutants, particularly salt, attract large mammals, putting them more at risk of being killed by vehicles (Fraser & Thomas 1982). Spills of edible products from trucks and trains also attract wildlife to roadsides. Finally, evolutionary processes may be affected through altered selection pressures that result in local differentiation of populations of both plants (Kiang 1982) and animals (Minoranskii & Kuzina 1984).

## Spread of Exotic Species

Roads provide dispersal of exotic species via three mechanisms: providing habitat by altering conditions, making invasion more likely by stressing or removing native species, and allowing easier movement by wild or human vectors. It is often difficult to distinguish among these factors. Soils modified during road construction can facilitate the spread of exotic plants along roadsides (Greenberg et al. 1997). Some exotic plants establish themselves preferentially along roadsides and in other disturbed habitats (Wester & Juvik 1983; Henderson & Wells 1986; Tyser & Worley 1992; Wein et al. 1992). The spread of exotic diseases (Dawson & Weste 1985; Gad et al. 1986) and insects (Pantaleoni 1989; Schedl 1991) is facilitated by increased density of roads and traffic volume. Road construction that alters the canopy structure of forests promotes invasion by exotic understory plants, which affects animal communities (Gaddy & Kohlsaat 1987). Some roadside verges have been invaded by maritime plants because of their ability to tolerate saline soil (Scott & Davison 1982). Feral fruit trees are found preferentially along roadsides, and some populations are maintained solely by seeds in fruit waste thrown from vehicles (Smith 1986).

Exotic species are sometimes introduced along roadsides for the purpose of erosion control (Niordson 1989). Native species are now more widely preferred for this purpose, but Dunlap (1987) argues that in some cases the need for rapid establishment of plant cover requires the use of exotic species.

In another form of deliberate introduction, roads provide easy access to streams and lakes for fishery managers to stock nonnative hatchery fish (Lee et al. 1997), which adversely affect native biota and disrupt aquatic ecosystems in many ways (Allan & Flecker 1993). Unsanctioned, illegal, and unintentional introductions of fishes, mollusks, plants, and other aquatic organisms also occur frequently (Allan & Flecker 1993), and they are facilitated by public road access to water bodies.

The dispersal of a biological agent such as a pathogen along a roadway can affect both terrestrial and aquatic ecosystems far from the road. In northern California and southwest Oregon, for example, vehicle traffic and roadway drainage along logging and mining roads during the wet season disperse spores of an exotic root disease (*Phythoptera lateralis*) that infects the endemic Port Orford cedar (*Chamaecyparis lawsoniana*; Zobel et al. 1985). Transfer of the water-borne spores from forest roads into headwater stream crossings can result in the infection and nearly complete mortality of Port Orford cedars along a much larger network of downstream channel margins and floodplains, even deep inside otherwise roadless areas. The progressive loss of this important conifer species from riparian ecosystems may engender substantial long-term consequences for the integrity of stream biota, including endangered salmon species, for which the Port Orford cedar provides shade, large and long-lasting coarse woody debris, and stabilization of channels and floodplains.

## Changes in Human Use of Land and Water

Roads facilitate increased use of an area by humans, who themselves often cause diverse and persistent ecological effects. New roads increase ease of access by humans into formerly remote areas. Perhaps more important, roads often increase the efficiency with which natural resources can be exported. At least three different kinds of human use of the landscape, made increasingly possible by roads, can have major ecological effects: hunting and fishing, recreation, and changes in use of land and water.

Roads open up areas to increased poaching and legal hunting. Hunting reduces population sizes of many game species, including brown bear (*Ursus arctos*; Camarra & Parde 1990), Iberian lynx (Ferreras et al. 1992), wolves (Fuller 1989), black bear (Manville 1983), and Egyptian mongooses (*Herpestes ichneumon*; Palomares & Delibes 1992). Roads also increase both legal and illegal fishing in streams and lakes. Native fish populations in previously inaccessible areas are often vulnerable to even small increases in fishing effort. Increased fishing then often gives rise to public demand for fish stocking as an attempt to artificially compensate for the effects of unsustainable harvest, at the further expense of native fishes and other species (e.g., Gresswell & Varley 1988).

Visitors increase when roads make areas more accessible, leading to increased passive harassment of animals—such as elk on Mount St. Helens in Washington State (Czech 1991) and the Oregon Coast Range (Witmer & DeCalesta 1985), brown bear in Europe (Del Campo et al. 1990), and mountain goats (*Oreamnos americanus*) in Montana (Pedevillano & Wright 1987)—and damage to plant communities (Matlack 1993).

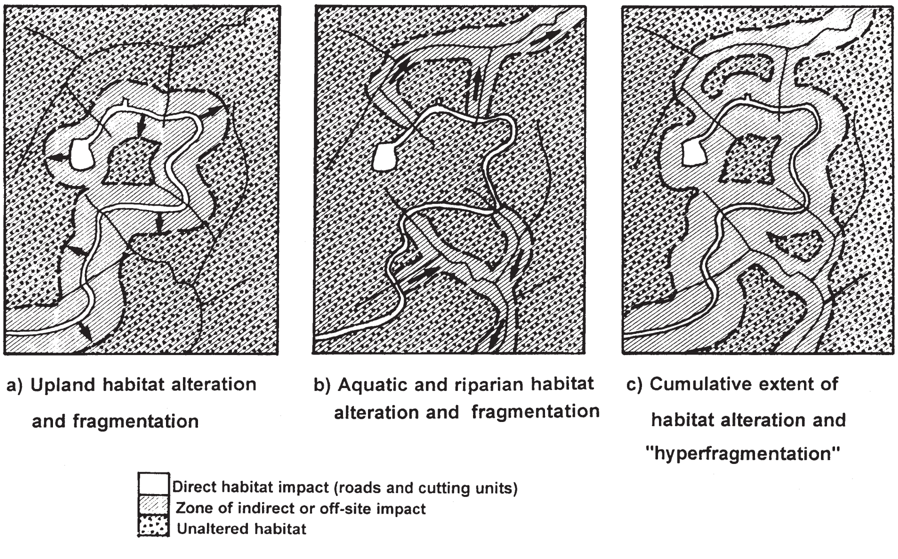
Roads are often built into areas to promote logging, agriculture, mining, and development of homes or industrial or commercial projects. Such changes in land cover and land and water use result in major and persistent adverse effects on the native flora and fauna of terrestrial (Van Dyke et al. 1986; Karnefelt & Mattsson 1989; P. Seibert 1993) and freshwater ecosystems (Schlosser 1991; Allan & Flecker 1993; Roth et al. 1996).

Numerous studies have demonstrated declines in stream health associated with roads. Because the nature and extent of land use within a region tend to be highly correlated with road networks, however, it is often difficult or impossible to separate the direct ecological effects of roads from those of the accompanying land-use activities. For example, Eaglin and Hubert (1993) reported that trout biomass and streambed habitat quality in Wyoming streams declined in relation to the number of road crossings and to the proportion of area logged in the contributing catchment. Findlay and Houlahan (1997) found that herptile species diversity in wetlands declined in relation to the density of roads within 2 km of the perimeter. Among streams in the Pacific Northwest, the status or abundance of bull trout populations has been inversely correlated to road density (Rieman et al. 1997; Baxter et al. 1999); these studies used roads as the best available general proxy of cumulative effects associated with land use and human access. On the other hand, some studies (e.g., Roth et al. 1996) have demonstrated correlations of stream biotic integrity with land-use patterns across large catchments but did not investigate the specific roles that roads might play in mediating the causes and effects.

It appears that roads can serve as useful indicators of the magnitude of land-use changes, but it remains unclear to what degree the associated ecological responses result directly from roads themselves. If roads are largely responsible, effects could be ameliorated through altered road design, placement, remediation, or road removal. Strong interactions between roads and land use are likely, however. Forest roads in Idaho, for example, are less prone to erosion when the surrounding landscape remains in natural forest cover (Seyedbagheri 1996).

## Discussion and Conclusions

Roads have diverse and systemic effects on many aspects of terrestrial and aquatic ecosystems. The ecological effects of roads can resonate substantial distances from the road in terrestrial ecosystems, creating habitat fragmentation and facilitating ensuing fragmentation through support of human exploitative activities (Fig. 1a). Habitat deterioration is not widely appreciated as an aspect of ecological fragmentation in aquatic ecosystems. At the scale of an extensive landscape or stream network, however, roads produce a pattern of aquatic habitat loss that differs from the terrestrial pattern yet nevertheless results in the ecological fragmentation of aquatic ecosystems (Fig. 1b). We coin the term *hyperfragmentation* to describe the multidimensional view of ecological fragmentation and habitat loss that emerges when the consequences of roads or any habitat alteration for terrestrial and aquatic ecosystems are considered simultaneously (Fig. 1c). Hyperfragmentation is the result of a spatial footprint of ecological effect that propagates across the landscape differently in freshwater and


a) Upland habitat alteration and fragmentation

b) Aquatic and riparian habitat alteration and fragmentation

c) Cumulative extent of habitat alteration and "hyperfragmentation"

*Figure 1. Spatial pattern of direct and indirect habitat alteration caused by human disturbance in a forested watershed: (a) classical forest edge effects contributing to terrestrial habitat fragmentation, (b) downstream-propagating hydrologic and biotic effects leading to large-scale fragmentation of freshwater habitats and populations, (c) combined terrestrial-aquatic view of landscape alteration that we term* hyperfragmentation *because it considers multiple ecosystem dimensions on the same landscape. Arrows indicate predominant spatial vector of effects.*

aquatic ecosystems than in terrestrial systems. Even where only a small percentage of the land's surface is directly occupied by roads, few corners of the landscape remain untouched by their off-site ecological effects. The breadth of these effects cannot be appreciated unless one takes a broadly transdisciplinary view of ecosystems and biological communities.

Road design, management, and restoration need to be more carefully tailored to address the full range of ecological processes and terrestrial and aquatic species that may be affected. Deliberate monitoring is necessary to ensure that projects have robust ecological benefits and minimal adverse effects and that they are cost-efficient relative to their actual benefits (e.g., Weaver et al. 1987). Of course, such assessments require time and money that are usually unavailable. Most funds used to remediate problem roads are earmarked for actual field operations and are not available to support such assessment and monitoring. Few of the experts building roads or "restoring" them are trained to recognize and address the full spectrum of ecological issues that we have identified. Moreover, by their nature roads have systemic ecological effects that, even if recognized, cannot be overcome.

If a broad view of the ecological effects of roads reveals a multiplicity of effects, it also suggests that it is unlikely that the consequences of roads will ever be completely mitigated or remediated. Thus, it is critical to retain remaining roadless or near-roadless portions of the landscape in their natural state. Because of the increasing rarity of roadless areas, especially roadless watersheds, conservation efforts cannot rely entirely on protection of existing natural areas. But neither can conservation efforts depend entirely on tenuous and unexamined assumptions about the capability of site- and species-specific mitigation and remediation measures to reduce the ecological consequences of existing and proposed roads.

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