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Road ecology: shifting gears toward evolutionary perspectives

Steven P Brady^{1*} and Jonathan L Richardson²

Recent advances in understanding the often rapid pace of evolution are reshaping our view of organisms and their capacity to cope with environmental change. Though evolutionary perspectives have gained traction in many fields of conservation, road ecology is not among them. This is surprising because roads are pervasive landscape features that generate intense natural selection. The biological outcomes from these selection pressures – whether adaptive or maladaptive – can have profound consequences for population persistence. We argue that studying evolutionary responses is critical to accurately understand the impacts of roads. Toward that end, we describe the basic tenets and relevance of contemporary evolution and showcase the few examples where it has been documented in road ecology. We outline practical ways that road ecologists can estimate and interpret evolutionary responses in their research. Finally, we suggest priority research topics and discuss how evolutionary insights can inform conservation in landscapes traversed by roads.

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An extensive road network exerts untold consequences on the planet. Roadkill, contamination from runoff, and fragmentation all challenge the success of populations in road-adjacent habitats (Forman and Alexander 1998; Trombulak and Frissell 2000). These and many other consequences are well described by the field of road ecology, which emerged two decades ago at a time when the ecological effects of roads were seldom considered (Forman *et al.* 2003). The field has since advanced steadily, gaining insights into both consequences and solutions (WebFigure 1). Road ecology institutes have been established, reviews have been published (eg Forman and Alexander 1998; Trombulak and Frissell 2000), and practical guides have been written (Andrews *et al.* 2015;

van der Ree *et al.* 2015). Yet amid this wealth of knowledge, one insight remains conspicuous by its absence: namely, evolutionary change caused by roads (Figure 1).

As demonstrated by many branches of conservation, neglecting evolutionary change in response to habitat modification prevents critical insights into a suite of complex, conservation-relevant responses (Carroll *et al.* 2014). Indeed, over the same 20-year period that road ecology has been proliferating, evolutionary perspectives have transformed insights in commercial fishing, climate change, invasive species, and ecotoxicology (Novak 2007; Norberg *et al.* 2012; Laugen *et al.* 2014; Hua *et al.* 2015). Relative to these contexts, road ecology lags behind the growing efforts to incorporate evolutionary perspectives in conservation (Figure 1). For example, a relatively recent book on road ecology – a 552-page volume – contains no mention of evolutionary consequences (van der Ree *et al.* 2015). Similarly, at the 2016 annual meeting of the Ecological Society of America, none of the 36 presentations mentioning roads referred to evolution. Compare this to a topic such as climate change, where hundreds of journal articles and several books describe evolutionary responses, and the contrast becomes very clear.

The need to understand and address evolutionary changes caused by roads is more pressing than ever. In the past decade, the global road network has more than doubled in size. Said to be the largest human artifact on the planet (Forman *et al.* 2003), the road network covers some 64,000,000 km of Earth's surface (CIA 2013), and is projected to increase 60% by 2050 (Dulac 2013). Here, we highlight why evolutionary perspectives are crucial for studying this vast and increasing road presence, noting that essential insights gained through road ecology can be used to examine potential selection pressures driving evolutionary change. We outline the conceptual basis for

In a nutshell:

- Roads are ubiquitous features of the landscape, affecting 20% of the US land area; globally, roads are projected to increase 60% in length by 2050
- The field of road ecology has described many of the negative effects of roads but has generally failed to consider their evolutionary consequences
- As shown in many other fields of conservation, evolutionary perspectives often transform our understanding of the ways organisms respond to environmental change
- The handful of evolutionary studies associated with roads reveals both positive and negative effects, indicating that evolution can increase or decrease the resiliency of road-affected populations
- Evolutionary perspectives are vital if we are to improve our capacity for understanding and addressing the pervasive effects of roads

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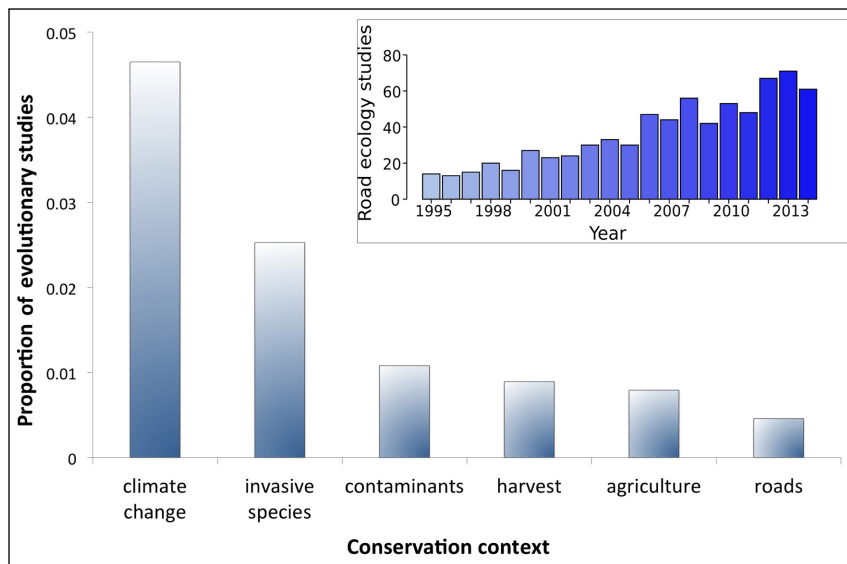


Figure 1. Distribution of conservation studies that test for contemporary evolution. The proportion of conservation studies referring to contemporary evolution is shown across a suite of conservation-relevant fields. The number of evolutionary studies is scaled to the number of conservation studies in each respective field. The number of road ecology studies (inset) has increased on average since the field emerged. Studies for each bar chart were found using a Web of Science search (WebTable 1).

implementing evolutionary perspectives, illustrate the few examples of road-induced evolutionary change, and discuss practical ways evolution can be incorporated into investigations of how roads influence natural systems. We hope this overview will aid and refine the development of an already vital field.

Despite an antiquated though persistent view that evolutionary change occurs exclusively over hundreds of millennia (Slobodkin 1961), we now know that evolution is a contemporary process that can effect change from one generation to the next (Hairston *et al.* 2005). Moreover, “contemporary evolutionary” effects can be as large as classical ecological effects (Hairston *et al.* 2005; Ellner *et al.* 2011; Schoener 2011) and can interact with ecological processes and feed back throughout ecosystems (Kinnison and Hairston 2007; Pelletier *et al.* 2009). While the nature of these changes depends on properties such as gene flow, genetic constraints, and generation time, evolution can proceed fast enough to modify the responses that road ecologists measure over periods of time that matter to conservation.

To appreciate the imperative for evolution in road ecology, ecologists must acknowledge that the environmental consequences of roads also act as agents of selection (Figure 2). Road effects are therefore the very forces that can drive evolutionary change, quickly and fundamentally altering organisms. Furthermore, because road effects themselves select for more fit individuals, the intensity of road-induced consequences can change as organisms evolve over time. For instance, road kill can become less prevalent as populations evolve to avoid

vehicle collisions (eg Brown and Bomberger Brown 2013). This combination of selection and dynamic responses is precisely why evolutionary perspectives are needed to fully describe the consequences of roads. Doing so will require a change in how we think about road effects, viewing organisms and their responses as dynamic rather than static.

■ Evolutionary change and its implications for roaded landscapes

Though much remains to be discovered about the long-term consequences of evolutionary responses to environmental change (Pelletier *et al.* 2009), it is clear that human-altered environments can drive contemporary evolution (Donihue and Lambert 2015). We outline the ways that evolution takes place, the patterns of adaptation and maladaptation that can result, and the conceptual framework for inferring evolutionary change, with the aim of building evolutionary perspectives in road ecology.

Mechanisms of change

Evolution is a change in the distribution of phenotypic traits – and the genes that underlie them – from one generation to the next. Though novel genetic mutations can occasionally facilitate this process, more often, genetic and phenotypic variation that already exists in populations is differentially propagated across generations via (1) random drift or (2) natural selection favoring adaptive phenotypes. We focus our discussion on selection because of its capacity to drive adaptation and induce maladaptation in response to environmental change, and because roads cause environmental changes that act as strong selective agents (see next section; Figure 2).

Adaptive change

Natural selection occurs when some heritable phenotypes (ie variants of a trait) have higher fitness, meaning individuals expressing those phenotypes survive and reproduce more successfully. The result is adaptation, represented by a shift in frequency toward traits with higher fitness. When selection pressures differ across populations, “local adaptation” may arise (Hereford 2009), wherein populations evolve higher fitness in their own environment relative to foreign populations exposed to that environment (Kawecki and Ebert 2004). For example, road-adjacent populations can evolve higher

tolerance to contaminants relative to populations located away from roads (eg Briggs 1972; Figure 3). Thus, organisms within populations that are negatively affected by roads may be able to reverse or mitigate decreased fitness and reproductive success through adaptation.

Notably, local adaptation reflects increased “relative fitness” of the local population. This means that local adaptation can occur even if population size (ie “absolute fitness”) decreases, as long as fitness remains higher than that of another population. In other words, a declining population is considered locally adapted if it declines at a slower rate (owing to evolution) relative to a foreign population exposed to that environment. Through evolution, such a locally adapted population might stabilize at a lower population size or recover to its original size through increased growth, provided there is sufficient adaptation. Alternatively, locally adapted populations may never stabilize numerically, despite some level of evolutionary adaptation. Local adaptation can therefore decrease the chance of, but does not preclude, local extinction.

Maladaptive change

Evolution can also be maladaptive, where relative fitness decreases in local populations. Maladaptation can occur for several reasons, even in the face of natural selection (Crespi 2000; Hendry and Gonzalez 2008). For instance, maladaptation may occur when selection is strong enough to decrease populations to sizes susceptible to inbreeding depression and/or the fixation of deleterious alleles via drift (Falk *et al.* 2012). Thus, an initially adaptive response to selection can subsequently be countered by the consequences of small populations, resulting in reduced fitness. Conversely, maladaptation can arise when gene flow arrives from foreign populations adapted to different selection pressures. Mutagenic effects can also induce maladaptation, for example in cases where environmental contaminants cause detrimental changes in genes (Lindberg *et al.* 2008).

Pace and spatial scale of change

The opposing outcomes of adaptation and maladaptation have different implications for conservation (for example, in terms of population status and triage of management efforts). Critically, these outcomes take place over short

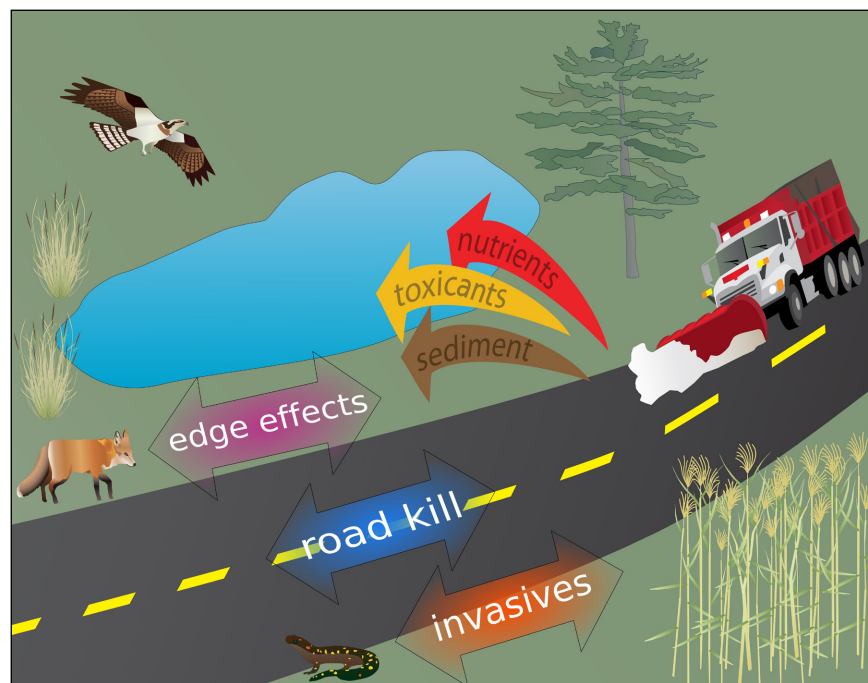


Figure 2. Roads as drivers of evolution. A suite of common ecological impacts of roads are shown as labeled arrows. While these effects are well described in road ecology, their role as known or likely agents of natural selection is poorly understood. Yet these factors are capable of driving contemporary evolutionary change. Studying the evolutionary effects of these factors will provide a more comprehensive understanding of the ways in which organisms are responding to the presence and consequences of roads.

timescales, leading to genetic and phenotypic change over just a few generations (Kinnison and Hendry 2001). Rates of change may be especially high in the context of human-altered environments, underscoring the relevance for roaded landscapes (Hendry *et al.* 2008). Relatedly, evolution proceeds over small spatial scales, well within dispersal distances (Richardson *et al.* 2014). This bears striking relevance to road studies: evolution can occur even at the fine scales at which roads bisect the landscape, and landscapes can become “checkered” with different evolutionary outcomes. For example, areas where roads are dense are also likely to contain groups of populations divergently evolved from those located away from roads, with adaptation and maladaptation resulting from diverse selection pressures. Indeed, natural selection can vary in patchy or continuous ways across landscapes, and both are relevant for selection imposed by roads. For instance, traffic noise is typically distributed as a continuous cline moving away from a road, whereas road salt is patchily distributed within drainage systems and basins adjacent to roads (Forman *et al.* 2003).

Plasticity, inherited environmental effects, and epigenetics

The combined pace of evolutionary change and the capacity of roads to induce those changes means that

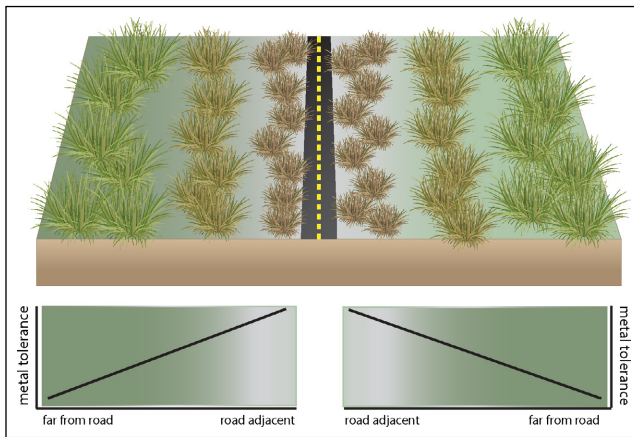


Figure 3. Local adaptation in plants adjacent to roads. The best evidence for road-induced evolution comes from plants, where local adaptation occurs when a roadside population has evolved higher fitness in its own environment relative to the fitness of a foreign population experimentally exposed to those same roadside conditions. Early studies showed that plants adjacent to roads are locally adapted to increased metal concentrations in the soil. Adaptive tolerance to these contaminants decreased with increasing distance from roads, corresponding to declines in both soil metal contamination and the strength of natural selection.

roaded landscapes can host numerous and diverse evolutionary outcomes. However, not all changes associated with selection reflect evolution. Rather, adaptive and maladaptive responses to selection pressures can also arise through phenotypic plasticity, wherein genetic composition remains the same but the environment induces different phenotypes (Fitzpatrick 2012). Such plasticity may also be passed from parent to offspring independent of their genes through environmentally induced inherited effects (eg maternal effects). Similarly, epigenetic effects – which describe changes in the ways genes are expressed – can persist through several generations without changing the underlying genotype. These mechanisms influencing trait variation are not mutually exclusive. Rather, trait variation is determined by the interaction of genetic and environmental components (known as the $G \times E$ interaction). While the genetic basis for certain traits is described in some model systems, phenotypic variation and the response to environmental change are highly context dependent (Merilä and Hendry 2014). The diverse nature of road effects and potential selection agents means that parsing these mechanisms requires well-designed experimental approaches.

■ Roads to evolution

Despite road ecology's relative lack of an evolutionary perspective, several important studies have reported

evolutionary change alongside roads (Figure 4). We highlight this work below, noting that despite large geographic and taxonomic variation, one clear commonality emerges: road-adjacent populations quickly become differentiated from nearby populations in their capacity to tolerate negative road effects. The earliest evidence for this effect was reported by Briggs (1972), who showed that road-adjacent populations of a liverwort (*Marchantia polymorpha*) evolved higher lead tolerance as compared to populations away from roads. Wu and Antonovics (1976) and Atkins *et al.* (1982) reported similar results in ribwort plantain (*Plantago lanceolata*) and a common grass (*Festuca rubra*), respectively (Figure 4). Kiang (1982) demonstrated that road-adjacent populations of another common grass (*Anthoxanthum odoratum*) evolved differences in morphology, flowering date, and fertility in less than 40 years, and increased tolerance to road salt in 30 years.

For three decades, no studies of road evolution followed these early reports. Recently, however, evidence indicates that effects can also be seen in vertebrates. Brown and Bomberger Brown (2013) found evidence for evolution in cliff swallows (*Petrochelidon pyrrhonota*) responding to selection from road-induced mortality. Over 30 years, the number of road-kill swallows decreased despite an increase in overall population size. At the same time, wing length of road-kill swallows increased while that of the overall population decreased. This suggests an evolved response to vehicle-associated selection favoring increased maneuverability and vertical takeoff achieved by shorter wings.

Roads can also simultaneously induce opposing outcomes of adaptation and maladaptation. This was the case reported for two amphibians – the spotted salamander (*Ambystoma maculatum*) and wood frog (*Rana sylvatica*) – breeding in identical roadside habitats (Brady 2012, 2013). Reciprocal transplant experiments (for a description, see next section and the Figure 5 caption) revealed a survival advantage of 25% for roadside populations of the spotted salamander compared to nearby populations located away from the road. Yet overall, the roadside environment was harsh, reducing survival by 35% as compared to more distant locations, highlighting the earlier point that relative fitness can increase locally even as absolute fitness decreases. For the wood frog, roadside populations were locally maladapted. In roadside ponds, local populations survived at 29% lower rates as compared to transplanted, non-adjacent populations. As with the salamanders above, the harsh roadside conditions reduced survival by 20% as compared to environments away from the road. These two amphibian species – characterized as ecologically similar – exhibited very different patterns of adaptive capacity to roadside environments, despite both being negatively affected by road proximity.

These studies suggest that tolerance to road effects evolves quickly, resulting in local population differentia-



Figure 4. Salient examples of evolutionary insights in road ecology. The few examples of evolutionary perspectives applied to road effects reveal consistently that populations are differentiated across small spatial and temporal scales. In most cases, populations appear to adapt; however, there is also evidence for maladaptation. (a) Red fescue (*Festuca rubra*) has evolved higher tolerance to lead pollution from roads; (b) cliff swallows (*Petrochelidon pyrrhonota*) have evolved shorter wings better suited to vertical takeoff as an apparent adaptation to avoid becoming road kill; (c) spotted salamanders (*Ambystoma maculatum*) are locally adapted to road adjacency; and (d) wood frogs (*Rana sylvatica*) show evidence for local maladaptation to road salt and road adjacency.

tion that can be either adaptive or maladaptive. Absent evolutionary perspectives, differences in tolerance would go undetected, making inference not only less precise but in some cases also qualitatively incorrect. For example, maladaptation in roadside wood frogs would not be detected by traditional ecological approaches, which might spuriously prompt the conclusion that roads cause about a 20% reduction in survival and no more. Instead, we know that roads can induce up to 57% relative mortality for roadside populations (Brady 2013). Inferences regarding spotted salamander responses would be similarly incorrect. While the negative effect from roads would be clear, the fact that local populations are adapting to these environments would be missed. Across studies, these insights suggest that many wild populations may evolve in response to roads, thus encouraging road ecolo-

gists to prioritize investigations involving road-induced evolution. In the following section, we briefly outline steps to accomplish this.

■ Where the rubber meets the road: applying evolutionary perspectives

Generating evolutionary inference

The first step in evaluating road-induced evolutionary change is to compare fitness between road-affected and unaffected populations. This “relative fitness” comparison is diagnostic of local adaptation and maladaptation. In some systems, fitness can be challenging to estimate (eg in long-lived organisms that breed infrequently). Instead, components of fitness (eg survival, fecundity)

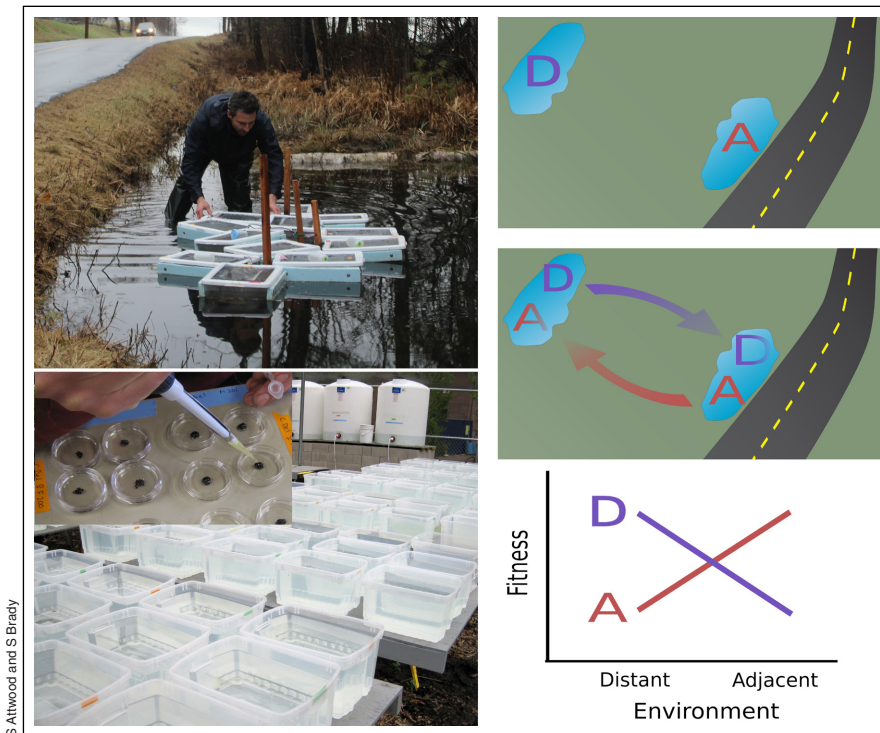


Figure 5. Experimental evolutionary techniques. Reciprocal transplant (top left) and common garden (bottom left) experiments are essential for evolutionary insights. Experiments can occur concomitantly, with related individuals represented in both venues, generating powerful understanding and suggesting potential mechanisms of selection. Artificial breeding experiments (bottom-left inset) are used to estimate heritability, including environmental and parental components. Reciprocal transplants utilize two or more populations (top right) to evaluate relative fitness, comparing the fitness of local versus foreign, transplanted populations (middle right). This allows additional inference into whether costs follow responses, for example in the form of a trade-off in fitness to a nearby environment (bottom right). In this example, experiments are conducted on populations that are road-adjacent (“A”) or distant from roads (“D”).

and performance traits (eg growth) can be used, assuming they are reasonable fitness predictors. Additionally, measures of traits hypothesized to influence fitness provide insight into the amount of variation available for selection, and the strength of that selection. For instance, does road kill select for faster individuals? And if so, what is the distribution of locomotor variation and how strongly favored is speed? Complementary measures of absolute fitness (ie change in population size) determine whether populations are stable, growing, or decreasing, and, together with relative fitness, can indicate whether adaptation and/or maladaptation are promoting stability, recovery, or decline.

Often, fitness and traits are measured in reciprocal transplant and common garden experiments (Figure 5). Both approaches are designed to reveal whether responses differ between populations by exposing individuals to common environmental conditions, either in lab settings (ie common garden experiment) or in the field (ie transplant experiment). Although uncommon,

multigenerational studies afford the most rigor for parsing genetic versus plastic effects while cross-breeding designs help pinpoint sources of effects between sexes and reveal genetic properties such as additive inheritance (Blanquart *et al.* 2013). Ultimately, linking traits to underlying genes provides the most complete understanding of evolutionary change (Stapley *et al.* 2010).

Priority topics for study

The potential to investigate road-induced evolution remains wide open. We suggest prioritizing contexts where selection is strong. Conveniently, these are likely contexts where negative ecological road effects are also strong, and should therefore align well with road ecology priorities. In any context where roads are known to modify traits, the potential exists for evolution to act on and mediate this variation. Systems where phenotypic changes have already been documented are exceptional starting points. Road noise, for example, may be an especially rich context, where trait changes in vertebrate taxa include declines in vocal activity (Lengagne 2008), increases in vocal pitch (Slabbekoorn and Peet 2003), and elevations in physiological stress (Tennessen *et al.* 2014). Similarly, changes in movement behavior associated with road crossing (Andrews and Gibbons 2005) are likely to be under strong selection.

Contexts demonstrating fitness consequences are also prime candidates. An obvious example is road kill (Clevenger *et al.* 2003), where natural selection might favor traits reducing the probability of being struck by vehicles. Indirect fitness effects, such as those caused by sub-lethal contaminant exposure or stress (Brand *et al.* 2010; Owen *et al.* 2014) can have similar implications for evolutionary change. Insights from non-roaded systems can also be instructive. For instance, knowledge of adaptive tolerance to salinity is well developed in fish models (Scott and Brix 2013), and may point to candidate traits and genes in fish and other taxa responding to road salt runoff. Finally, systems where roads impede gene flow (Epps *et al.* 2005; Marsh *et al.* 2008; Clark *et al.* 2010) might be especially profitable, as reduced gene flow can both hasten adaptation by reducing maladaptive genetic load and facilitate maladaptation by inducing inbreeding

depression and/or genetic drift (Garant *et al.* 2007; Richardson *et al.* 2016).

Translating insights to management

Using the techniques outlined above, identifying whether road-adjacent populations have become adapted or maladapted can help triage conservation priorities and determine specific tactics to improve population success. For example, well-adapted road-adjacent populations could be used to benefit struggling populations by promoting gene flow or through assisted migration (Whiteley *et al.* 2015). Conservation strategies for maladapted populations would require information on the levels of genetic variation available for adaptation, the degree to which individuals can move among populations (ie connectivity), and gene flow exchanged with populations facing different selection pressures. In the lattermost case, one conservation tactic may be to inhibit rather than encourage connectivity between those dissimilar habitats.

More generally, when incorporating evolutionary insights into management, one should consider the goals for particular landscapes, populations, or species. Strategies might focus on maximizing connectivity among habitats, preserving genetic diversity, bolstering population sizes, and/or supporting adaptive potential in future environments by maintaining phenotypic variation. The most comprehensive management strategies take all of these factors into account; however, in practice, certain goals may be given higher priority. For example, where climate change threatens Hawaiian honeycreepers through increased spread of avian malaria (Atkinson *et al.* 2013), an evolutionary-based recommendation is to facilitate evolution of malarial resistance by controlling predacious rodents, thus fostering honeycreeper population size and adaptive potential (Kilpatrick 2006).

Integrating evolutionary concepts into management and policy has been the focus of recent syntheses addressing environmental degradation, food production, human health, and climate change (eg Carroll *et al.* 2014). We anticipate that extending this use of evolution to road ecology will lead to a more comprehensive and effective field of study and conservation strategies. Ultimately, knowledge of adaptive and maladaptive outcomes will lead to an improved understanding of potentially cryptic road effects, allowing scientists and their partners in management and policy to identify more accurate and nuanced actions to mitigate the consequences of roads.

Conclusion

Conservation science is being transformed by evolutionary perspectives. We hope to galvanize a similar transformation in road ecology. Evolutionary changes shape the responses that road ecologists study while fundamentally altering the biology of organisms, profoundly affecting

their fate over timescales relevant to conservation. As we broaden our understanding of the contemporary dynamics of adaptation and maladaptation, so too will we increase our capacity to predict and mitigate negative road effects. Indeed, studying the mutual interaction between the road network and evolutionary change promises to provide a more thorough understanding of the complex effects that roads exert on our planet, the way that organisms respond, and the strategies necessary to mitigate road effects on natural systems.

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References

- Andrews KM and Gibbons JW. 2005. How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia* 2005: 772–82.
- Andrews KM, Nanjappa P, and Riley SP (Eds). 2015. Roads and ecological infrastructure: concepts and applications for small animals. Baltimore, MD: Johns Hopkins University Press.
- Atkins DP, Trueman IC, Clarke CB, and Bradshaw AD. 1982. The evolution of lead tolerance by *Festuca rubra* on a motorway verge. *Environ Pollut A* 27: 233–41.
- Atkinson CT, Saili KS, Utzurrum RB, and Jarvi SI. 2013. Experimental evidence for evolved tolerance to avian malaria in a wild population of low elevation Hawai'i 'Amakihi (*Hemignathus virens*). *EcoHealth* 10: 366–75.
- Blanquart F, Kaltz O, Nuismer SL, and Gandon S. 2013. A practical guide to measuring local adaptation. *Ecol Lett* 16: 1195–205.
- Brady SP. 2012. Road to evolution? Local adaptation to road adjacency in an amphibian (*Ambystoma maculatum*). *Sci Rep* 2: 235; doi:10.1038/srep00235.
- Brady SP. 2013. Microgeographic maladaptive performance and deme depression in a fragmented landscape. *PeerJ* 1: e163.
- Brand AB, Snodgrass JW, Gallagher MT, *et al.* 2010. Lethal and sublethal effects of embryonic and larval exposure of *Hyla versicolor* to stormwater pond sediments. *Arch Environ Con Tox* 58: 325–31.
- Briggs D. 1972. Population differentiation in *Marchantia polymorpha* L in various lead pollution levels. *Nature* 238: 166–67.
- Brown CR and Bomberger Brown M. 2013. Where has all the road kill gone? *Curr Biol* 23: R233–34.
- Carroll SP, Jørgensen PS, Kinnison MT, *et al.* 2014. Applying evolutionary biology to address global challenges. *Science* 346; doi:10.1126/science.1245993.
- CIA (Central Intelligence Agency). 2013. The world factbook 2013–14. Washington, DC: CIA.
- Clark RW, Brown WS, Stechert R, and Zamudio KR. 2010. Roads, interrupted dispersal, and genetic diversity in timber rattlesnakes. *Conserv Biol* 24: 1059–69.
- Clevenger AP, Chruszcz B, and Gunson KE. 2003. Spatial patterns and factors influencing small vertebrate fauna road-kill aggregations. *Biol Conserv* 109: 15–26.
- Crespi BJ. 2000. The evolution of maladaptation. *Heredity* 84: 623–29.
- Donihue C and Lambert M. 2015. Adaptive evolution in urban ecosystems. *Ambio* 44: 194–203.
- Dulac J. 2013. Global land transport infrastructure requirements: estimating road and railway infrastructure capacity and costs to 2050. Paris, France: International Energy Agency.

- Ellner SP, Geber MA, and Hairston NG. 2011. Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecol Lett* **14**: 603–14.
- Epps CW, Palsbøll PJ, Wehausen JD, et al. 2005. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. *Ecol Lett* **8**: 1029–38.
- Falk JJ, Parent CE, Agashe D, and Bolnick DI. 2012. Drift and selection entwined: asymmetric reproductive isolation in an experimental niche shift. *Evol Ecol Res* **14**: 403–23.
- Fitzpatrick BM. 2012. Underappreciated consequences of phenotypic plasticity for ecological speciation. *Int J Ecol* **2012**; art256017.
- Forman RTT and Alexander LE. 1998. Roads and their major ecological effects. *Annu Rev Ecol Syst* **29**: 207–31.
- Forman RTT, Sperling D, Bissonette J, et al. 2003. Road ecology: science and solutions. Washington, DC: Island Press.
- Garant D, Forde SE, and Hendry AP. 2007. The multifarious effects of dispersal and gene flow on contemporary adaptation. *Funct Ecol* **21**: 434–43.
- Hairston NG, Ellner SP, Geber MA, et al. 2005. Rapid evolution and the convergence of ecological and evolutionary time. *Ecol Lett* **8**: 1114–27.
- Hendry AP and Gonzalez A. 2008. Whither adaptation? *Biol Philos* **23**: 673–99.
- Hendry AP, Farrugia TJ, and Kinnison MT. 2008. Human influences on rates of phenotypic change in wild animal populations. *Mol Ecol* **17**: 20–29.
- Hereford J. 2009. A quantitative survey of local adaptation and fitness trade-offs. *Am Nat* **173**: 579–88.
- Hua J, Jones DK, Mattes BM, et al. 2015. Evolved pesticide tolerance in amphibians: predicting mechanisms based on pesticide novelty and mode of action. *Environ Pollut* **206**: 56–63.
- Kawecki TJ and Ebert D. 2004. Conceptual issues in local adaptation. *Ecol Lett* **7**: 1225–41.
- Kiang YT. 1982. Local differentiation of *Anthoxanthum odoratum* L populations on roadsides. *Am Midl Nat* **107**: 340–50.
- Kilpatrick AM. 2006. Facilitating the evolution of resistance to avian malaria in Hawaiian birds. *Biol Conserv* **128**: 475–85.
- Kinnison MT and Hairston NG. 2007. Eco-evolutionary conservation biology: contemporary evolution and the dynamics of persistence. *Funct Ecol* **21**: 444–54.
- Kinnison MT and Hendry AP. 2001. The pace of modern life II: from rates of contemporary microevolution to pattern and process. *Genetica* **112**: 145–64.
- Laugen AT, Engelhard GH, Whitlock R, et al. 2014. Evolutionary impact assessment: accounting for evolutionary consequences of fishing in an ecosystem approach to fisheries management. *Fish Fish* **15**: 65–96.
- Lengagne T. 2008. Traffic noise affects communication behaviour in a breeding anuran, *Hyla arborea*. *Biol Conserv* **141**: 2023–31.
- Lindberg HK, Väänänen V, Järventaus H, et al. 2008. Genotoxic effects of fumes from asphalt modified with waste plastic and tall oil pitch. *Mutat Res-Genet Tox En* **653**: 82–90.
- Marsh D, Page R, Hanlon T, et al. 2008. Effects of roads on patterns of genetic differentiation in red-backed salamanders, *Plethodon cinereus*. *Conserv Genet* **9**: 603–13.
- Merilä J and Hendry AP. 2014. Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. *Evol Appl* **7**: 1–14.
- Norberg J, Urban MC, Vellend M, et al. 2012. Eco-evolutionary responses of biodiversity to climate change. *Nature Clim Change* **2**: 747–51.
- Novak SJ. 2007. The role of evolution in the invasion process. *P Natl Acad Sci USA* **104**: 3671–72.
- Owen DAS, Carter ET, Holding ML, et al. 2014. Roads are associated with a blunted stress response in a North American pit viper. *Gen Comp Endocr* **202**: 87–92.
- Pelletier F, Garant D, and Hendry AP. 2009. Eco-evolutionary dynamics. *Philos T Roy Soc B* **364**: 1483–89.
- Richardson JL, Brady SP, Wang IJ, and Spear SF. 2016. Navigating the pitfalls and promise of landscape genetics. *Mol Ecol* **25**: 849–63.
- Richardson JL, Urban MC, Bolnick DI, and Skelly DK. 2014. Microgeographic adaptation and the spatial scale of evolution. *Trends Ecol Evol* **29**: 165–76.
- Schoener TW. 2011. The newest synthesis: understanding the interplay of evolutionary and ecological dynamics. *Science* **331**: 426–29.
- Scott GR and Brix KV. 2013. Evolution of salinity tolerance from transcriptome to physiological system. *Mol Ecol* **22**: 3656–58.
- Slabbekoorn H and Peet M. 2003. Ecology: birds sing at a higher pitch in urban noise. *Nature* **424**: 267.
- Slobodkin L. 1961. Growth and regulation of animal populations. New York, NY: Holt, Rinehart, and Winston.
- Stapley J, Reger J, Feulner PG, et al. 2010. Adaptation genomics: the next generation. *Trends Ecol Evol* **25**: 705–12.
- Tennessen JB, Parks SE, Langkilde T. 2014. Traffic noise causes physiological stress and impairs breeding migration behaviour in frogs. *Conserv Physiol* **2**: cou032.
- Trombulak SC and Frissell CA. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. *Conserv Biol* **14**: 18–30.
- van der Ree R, Smith DJ, and Grilo C (Eds). 2015. Handbook of road ecology. Chichester, UK: John Wiley & Sons.
- Whiteley AR, Fitzpatrick SW, Funk WC, and Tallmon DA. 2015. Genetic rescue to the rescue. *Trends Ecol Evol* **30**: 42–49.
- Wu L and Antonovics J. 1976. Experimental ecological genetics in *Plantago* II. Lead tolerance in *Plantago lanceolata* and *Cynodon dactylon* from a roadside. *Ecology* **57**: 205–08.

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