Fence Ecology: Frameworks for Understanding the Ecological Effects of Fences

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Investigations of the links between human infrastructure and ecological change have provided eye-opening insights into humanity's environmental impacts and contributed to global environmental policies. Fences are globally ubiquitous, yet they are often omitted from discussions of anthropogenic impacts. In the present article, we address this gap through a systematic literature review on the ecological effects of fences. Our overview provides five major takeaways: 1) an operational definition of fencing to structure future research, 2) an estimate of fence densities in the western United States to emphasize the challenges of accounting for fences in human-footprint mapping, 3) a framework exhibiting the ecological winners and losers that fences produce, 4) a typology of fence effects across ecological scales to guide research, and 5) a summary of research trends and biases that suggest that fence effects have been underestimated. Through highlighting past research and offering frameworks for the future, we aim with this work to formalize the nascent field of fence ecology.

Keywords: fence ecology, linear infrastructure, connectivity, anthropogenic impacts, socioecological systems

Fences are one of the most widespread manmade features on Earth, and they may outstretch roads by an order of magnitude (Jakes et al. 2018). Although recent popular attention on border fences has made headlines—Europe, for example, now has more kilometers of border fencing than it did during the cold war (Vallet 2016)—these barriers represent only a tiny fraction of a rapidly spreading global network of fences. Unlike roads and other forms of linear infrastructure, there exists no formal research synthesis on the fences that encircle our planet (Forman et al. 2003, Fahrig and Rytwinski 2009, van der Ree et al. 2015). However, recent case studies have charted local explosions of fencing and the dangerous social and ecological collapses that can follow (Hoole and Berkes 2010, Løvschal et al. 2017). Studies such as these have prompted calls for focused investigations into the potentially devastating and undiscovered consequences of fencing and for new frameworks to guide research and management (Sutherland et al. 2013, Jakes et al. 2018).

Calls for research into the ecological impacts of fences, however, are set against the long history of fences as a tool for managing and even protecting wildlife and habitat. In New Zealand and Australia, fences have famously provided lines of defense against harmful invasive species (Moseby and Read 2006). In Africa, numerous publications have made the case both for and against fencing for conservation (Hayward et al. 2007, Creel et al. 2013, Packer et al. 2013, Woodroffe et al. 2014, Durant et al. 2015), whereas in North America and Europe, researchers have proposed innovative forms of fencing with the goal of reducing wildlife–vehicle collisions (Clevenger et al. 2001, Klar et al. 2009). Throughout the world, land managers and restoration ecologists have successfully employed fences to protect and rehabilitate fragile habitats, especially from the impacts of livestock and invasive species (Spooner et al. 2002, Denmead et al. 2015). Fences therefore have the ability to both benefit and harm the ecosystems in which they occur, making the absence of systematic studies of their ecological effects all the more glaring.

Fences have eluded systematic study for so long for good reason. Fences are both difficult to detect, and, at an even more basic level, difficult to define. Fencing has become a popular metaphor in many disciplines, from ecology to computing. Even within ecological studies of fencing, there is considerable semantic drift in what constitutes a fence, as we discuss further below. Where fences have been sufficiently defined, unlike many other forms of infrastructure, they can evade detection, even by sophisticated imagery-driven methods that underpin many global change assessments (Poor et al. 2014). As a result, fences are often framed as a management tool rather than a globally significant ecological feature, and they are a notable omission from efforts to

BioScience 70: 971–985.
doi:10.1093/biosci/biaa103
Advance Access publication 30 September 2020

map global infrastructure, including the human footprint (Sanderson et al. 2002). The great variation in composition, structure and function of fences further complicates efforts to summarize their effects. Taken together, these factors may explain how we have few general lessons or even broad approaches to understanding the ecological consequences of one of the most ubiquitous products of human civilization.

A recent study by Jakes and colleagues (2018) introduced the need to establish the underpinning of a subdiscipline of fence ecology that can identify fences, locate them spatially, unpack their striking or subtle impacts, and direct research. In the present article, we build on the work of Jakes and colleagues (2018) by conducting a systematic literature review on fences to show that the effects of fences are complex, widespread, and still poorly understood. We offer five major takeaways from this research. First, we present an operational definition of fencing to maintain focus on the most widespread and impactful features meriting discussion. We discuss the important variation in type and scale of fences even within this definition, as well as the significance of construction and deterioration of fences over time. Second, we comment on the difficulties in mapping fences and their impacts, which have likely delayed meaningful large-scale assessments of ecological outcomes. We provide one of the first large-scale estimates of fence density in the western United States (box 1) to demonstrate how fences might alter well-established spatial estimates of human impacts (Leu et al. 2008). Third, we show that the diverse consequences of fences are not strictly beneficial or harmful and instead vary widely by species, system, and context. We offer a guide to predicting common “winners and losers” in a fenced world. Fourth, we present a typology of the potential impacts of fences at every scale of ecological analysis and show that a large body of idiosyncratic literature on fences has demonstrated diverse effects (Gadd 2011). We propose this typology as an organizing framework to help prioritize future research. Fifth and finally, we show that surprising trends and biases characterize the existing body of literature on fences, and that these trends and biases mask the full gamut of fence effects. A predictive and comprehensive fence ecology demands further research to address these shortfalls.

What is a fence?

A recent call to action by Jakes and colleagues (2018) defined *fence ecology* as the interactions between fences, wildlife, ecosystems, and societal needs. We propose to expand this definition to include all organisms beyond just wildlife. Nevertheless, with this modification, we believe the definition above offers a succinct and useful summation of what fence ecology might come to include. To facilitate the development of fence ecology into a subdiscipline of its own, a clear and concise definition of what constitutes a fence is first needed. The diversity of tools and approaches that go by the name *fence*, as well as those qualifying features that go by other names, make this task more difficult than it seems. How, for example, does a fence differ from a wall, and are such differences ecologically significant? Should innovative tactics in the realm of human–wildlife interactions, such as bee, chili pepper, or sonic “fences” be considered fences? If *fence* represents everything from a 10-meter-thick wall separating nations to the strategic placement of beehives, can we realistically draw conclusions about their effects? We believe the answer is no, and that a narrower definition is required for consistency and clarity.

We define a fence as a physical linear feature with vertical load-bearing components (e.g., poles) and noncontinuous structures (e.g., boards, wires, rails, nettings) spanning these vertical components (figure 1). Although this definition narrows the conversation, it still covers a great diversity of fences. Fences are differentially permeable to species and processes, and may be quickly constructed and deconstructed by people. This definition excludes walls, which are typified by completely solid features rather than intermittent components and which may impose a different set of effects than fences because of their opacity and impermeability. Bee, chili, and sonic fences, mentioned above, are characterized by nonlinear shapes and do not feature physical structural components and therefore also do not fit our definition of “fence.” Neither do hedgerows or other intentional uses of vegetation to structure space. Although some ecological effects of these non-fence barriers may resemble the effects of fences as defined in the present article, others will differ markedly, as will the mechanisms underlying their effects. For this reason, we will abide by the specific definition of a fence mentioned above, a description that allows a common lens to examine the vast majority of ecological impacts of fences throughout the world.

Temporal dynamics of fencing. Though often considered spatially, there are important temporal considerations when it comes to assessing the ecological consequences of fences. Compared with many other types of infrastructure, fences are much faster to construct, and fence proliferation is occurring rapidly around the world, with short-term functionality prioritized over long-term consequences (Linnell et al. 2016, Sun et al. 2020). Construction of new fences also frequently accompanies shifting systems of land tenure (Li WJ et al. 2007, Evans and Adams 2016). In many areas of the world, especially developing areas, privatization and subdivision of land is increasingly common (Yan and Wu 2005). Fences are a primary tool in manifesting and enforcing these changing policies (Yeh 2005, Richard et al. 2006, Said et al. 2016). As with many ecological phenomena, the pace of change is an essential consideration for understanding impacts, and it is no different with fences. Recent documentation of extreme rates of fence growth in Africa, for example, hint that the pace of change has thwarted the ability of species and systems to adapt, resulting in local ecosystem collapse (Løvschal et al. 2017).

Although fences may be established rapidly, they can also deteriorate quickly, which adds to their dynamic

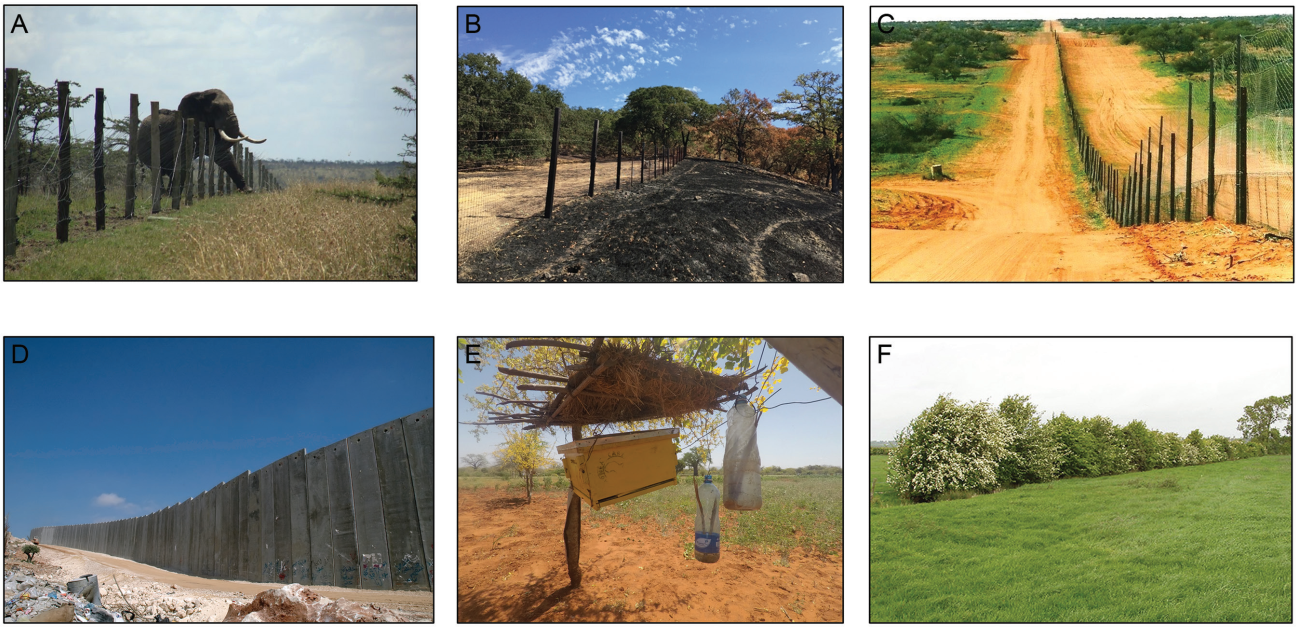

Figure 1. Fence or not a fence? Fences require a specific and broadly applicable definition to allow for the establishment of consistent methods and frameworks in fence ecology. In the present article, we define a fence as a physical linear feature with vertical load-bearing components and noncontinuous structures spanning these vertical components. Examples of structures fitting this definition include (a) an electrified elephant fence in Kenya (photograph: Lauren Evans, Space for Giants), (b) a woven wire livestock fence in California (photograph: the Hopland Research and Extension Center), and (c) a dingo fence in Australia (photograph: Peter Woodward). Examples of structures not fitting this definition include (d) a border wall between Israel and Palestine (photo by Justin McIntosh), (e) a honey bee fence in Kenya (photograph KenGee8), and (f) a hedgerow in England (photograph: David Hawgood).

nature and the difficulty in quantifying their extent and impact. The level of maintenance or decay of a fence is essential to its effectiveness at its intended purpose and may drastically change its ecological effects (Pirie et al. 2017). Keeping fences maintained has long been a central occupation of pastoralists, but now other fence builders have come to understand its importance. Conservationists, for example, have found that invasive species rapidly discover and exploit breaks in fences (Connolly et al. 2009), undercutting their purpose when regular maintenance is not possible (McKnight 1969, Dube et al. 2010, Scofield et al. 2011, Kesch et al. 2014). Therefore, even where fences can be mapped, either remotely or via ground surveys, characterizing their intactness or functionality requires a closer, and often infeasible, form of evaluation.

Even with the restrictive definition of fencing we provide, fences vary widely in their physical characteristics, spatial distribution, and construction and decay over time. This variation leads to a diversity of consequences, as we discuss below, and points to the need for both guiding frameworks and context-specific research, including more systematic documentation of fence characteristics and locations around the world. Below we define a typology of fence impacts for fences to help manage this complexity.

Winners and losers in a fenced world

A debate about whether fences are beneficial or harmful to the conservation of systems in which they occur has raged for decades (Hayward and Kerley 2009, Creel et al. 2013, Packer et al. 2013, Woodroffe et al. 2014, Durant et al. 2015). Jakes and colleagues (2018) argued that fences may have dichotomous ecological effects, so we conducted a systematic literature review to better understand the diverse impacts of fences and whether and how they benefit or harm the systems in which they occur (see the supplemental material).

Unsurprisingly, the answer to this question is nuanced. Our review of 446 studies published from 1948 to 2018 showed that fences neither unequivocally protect nor harm ecosystems. The effects of fences on their ecological surroundings are diverse, and the same fence can be both beneficial and detrimental depending on species, scale, and type of effect considered. For example, several studies have shown that conservation fences in Africa may protect vulnerable wildlife species from poaching and other human impacts, but, if aligned unfavorably, they may also prohibit the same species from accessing essential resources such as watering holes (Ferguson and Hanks 2010). Given this, we suggest that fence ecology should consider not just the blatantly deleterious consequences of fences, but rather take a

Box 1. Invisible fences, invisible impacts.

Fences are a globally ubiquitous feature. They have accompanied human settlements for millennia, but they also occur in remote, unsettled areas to delineate boundaries or cordon livestock. Unlike roads, which modern cartographic and remote sensing technologies can typically detect (Mnih and Hinton 2010), most of the world's fences remain uncharted, and we found no large-spatial-scale and few small-spatial-scale efforts to map fences. Where recent research has attempted remote sensing of fences, evidence suggests that fences may outstrip roads substantially (Poor et al. 2014, Jakes et al. 2018). Furthermore, because fencing materials have become cheaper and more widely available, their use is accelerating. For example, the practice of fencing roads is increasingly common, both to mitigate wildlife–vehicle strikes, but also to manage snow drifts, and has now become standard practice in many countries (Peaden et al. 2017). The rapid increase in fencing further highlights the importance of understanding their effects on nature.

Although it may be difficult to map the dynamic global network of fences, it is possible to make meaningful estimates about fence densities where data is available. We estimated the length of fencing and fence densities in the western United States using a conservative model to predict the presence of fences. We followed methods and assumptions developed by Poor (2014), but implemented these methods at a large spatial scale that spans multiple ecosystems. At this spatial scale, we could not identify all private property boundaries, because parcel data for the region is incomplete. However, most boundaries at this scale are defined by or against the boundaries in federal lands, which cover more than half of the land area in this region (Vincent et al. 2017). Within federal lands, grazing makes up the primary land use (Bigelow and Borchers 2017), and we combined data on federal pasture boundaries with federal property boundaries to determine rural grazing fence distribution (BLM 2018). We also assumed primary and secondary roads would be fenced, and included these in our analysis (USCB 2019). We did not attempt to model fence densities in urban or suburban areas, where other types of infrastructure and land use would likely complicate or outweigh the impacts of fences.

Our model estimated over 1 million kilometers (km) of fences in the western United States, without including urban and suburban property fences. We calculated a kernel density surrounding these fence approximations at a distance of 50 (km), which was greater than the largest distance from any given point in the region to its nearest fence (figure 2a). The furthest distance from any fence was calculated at 48 (km), with a mean of 3.1 (km) from a fence for the region.

As expected, this model shows high densities of fencing around urban areas, with lower densities characterizing most rural and remote parts of the western United States. However, several areas stood out as having high densities of fencing despite their remoteness from human settlements. We compared this fence density map with the human footprint in the western United States (Leu et al. 2008) and highlighted regions where fence densities are high, but the human footprint is low (figure 2b). Several areas of high fence density and low estimated human footprint reiterate the point that the extent of ecological impacts of fences on species and systems have likely yet to be captured by models and approaches attempting to understand global change. All calculations in this box were conducted using ArcMap (ESRI 2018).

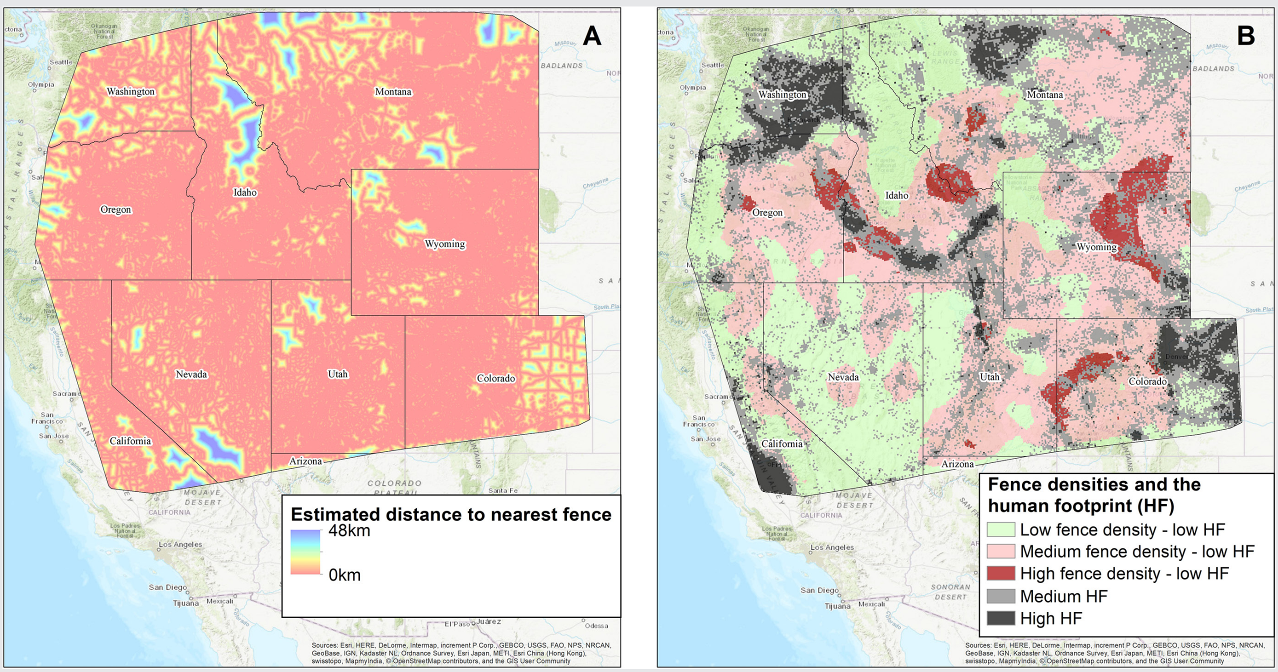

Figure 2. A large-spatial-scale analysis of the spatial extent of fencing in the western United States. We assembled a conservative data set of potential fence lines and (a) calculated the nearest distance to any given fence to be less than 50 kilometers, with a mean of 3.1 kilometers, and (b) identified areas of medium and high fence densities whose human footprint has likely been underestimated.

broader view that fences reorganize the species and systems in which they occur. To put it simply, in a fenced world, there are winners and there are losers (table 1).

In the sections below, we describe general trends that typify the ecological winners and losers of a fenced world. We define winners as species, communities, or systems for which the conditions supporting long-term survival and functioning improve; losers conversely are species, communities, or systems facing impediments to survival and functioning because of fences. We discuss trends first by species but note that the focus on species-level effects of fences is a significant and potentially dangerous bias, to which we will return later in this article. We also discuss traits, species, and systems that tend to become winners or losers, according to our review of the literature.

Our literature review clearly demonstrates the critical point that even where fences create winners, they simultaneously produce losers at different scales and under different contexts. This is an essential but often overlooked outcome of fence construction.

Fence purposes and their outcomes. Although the existing literature on fences has likely not captured all of the diverse effects of fences, major patterns and examples of winners and losers emerged from our review (table 1). One of the most notable patterns, which deserves greater research, is that many fences create winners and losers on the basis of the intentions of the fence builders (supplemental table S1). In other words, when fences are built for a specific species and purpose, they often achieve that purpose. Conservation and restoration fences, for example, have support within the literature for their beneficial effects for wildlife and sensitive plant species for which they are built, making such species “winners” in the fencing game. On the other hand, there is a critical lack of information on species that are not the targets for which fences are built, and our review shows that only 10.8% (48 of 446) of studies focus on nontarget species (supplemental table S2). To give a real-world example, a conservation fence in southeastern Australia effectively prevented the ingress of target pest species to an enclosed nature reserve. However, the same fence was found to have unintended negative consequences for native reptile populations around the enclosure, especially for eastern long-necked turtles (*Chelodina longicollis*). The fence disrupted turtle movement patterns, isolated populations, and led to high mortality rates when turtles were entangled in fences, demonstrating one cost of otherwise successful fences on nontarget species (Ferronato et al. 2014). Even when the intentions of fences are benign, their effects on nontarget species can create losers, and more research is required to understand the extent of these impacts.

Other examples from our review emphasized further the risks of targeting the use of fences in management solely on focal species. One study unpacked this complexity by examining a fence that was removed between adjacent nature reserves in South Africa. Although this fence removal was initially proclaimed a success by enlarging a protected area and increasing connectivity for wildlife, there were differential outcomes for different species. After fence removal, management focused on the charismatic Big 5 wildlife species originally found only in the larger of the two reserves. As a result, less charismatic obligate grazer species such as sable (*Hippotragus niger*), roan (*Hippotragus equinus*), tsessebe (*Damaliscus lunatus*), and eland (*Taurotragus oryx*) that had been thriving in the smaller fenced reserve declined in spite of fence removal, because the new management regime favored more charismatic species (Child 2010). As this study demonstrates, often the clearest winners because of fencing are the species that humans value most, whereas losers are inevitable but may remain invisible.

Species-level predictors of winners and losers. Our literature review also revealed trends that were independent of fence purposes or management goals. Broadly speaking, fences favor generalists and disturbance specialists, many of which are invasive, as well as small and small-ranged, nonmigratory species. Fences therefore heavily restrict what makes a species a winner. We review these trends in more detail in the present article.

As with many kinds of infrastructure, generalists and disturbance specialists become winners in a fenced world. For specialist species, fences can restrict access, change the community composition, or otherwise alter the ecology of systems on which they depend. At a larger scale, specialized systems with sensitive dependence on component species or species interactions, are also more likely to experience state shifts because of fencing, according to trends found in this review. Conversely, generalist species, and especially disturbance specialists, may readily adapt to the nested scales of impacts that fences create. For example, multiple studies point to generalist bird species already adapted to roadside areas or agricultural systems, such as the red-winged blackbird (*Agelaius phoeniceus*), loggerhead shrike (*Lanius ludovicianus migrans*), or great tit (*Parus major*), actively incorporating fences into their habitats (Camp and Best 1994, Lesiński 2000, Eseley and Bollinger 2001).

Many invasive species also readily adapt to novel or disturbed habitats. Therefore, although many fences targeted toward the prevention of the spread of invasive species have a demonstrated record of success, other kinds of fences facilitate invasive species (Conway and Nordstrom 2003, Brown et al. 2006, Loo et al. 2009). In a particularly ironic case in Australia, fences, a favored tool for limiting invasive species in the country, facilitated the movement of invasive cane toads (*Bufo marinus*) along cleared fence lines (Brown et al. 2006). Comparatively little research has been conducted on the potential of fences to foster species invasions, and this topic deserves much greater research attention.

Highly mobile animals are more likely to encounter fences and become exposed to their dangers, even in areas in which fences may otherwise provide benefits. Within conservation fences for example, large mobile species with large range

Table 1. Characteristics of fences, including purpose, features, extent, and ecological winners and losers.

Fence purpose	Typical fence characteristics	Winners	Losers	Extent
Conservation or restoration (e.g., fenced reserves)	• Closed • Expensive • Impermeable to people or livestock • Impermeable to target species • Paired with focused management	• Sensitive species where human or livestock impacts are likely • Species or systems whose biology or phenology allows them to thrive within a closed fence (e.g., smaller ranged species, small self-contained ecosystems) • Marketable or charismatic species who benefit from management in a closed system • Pathogens and parasites reliant on dense contact networks • "Pest" species that are difficult to eradicate, which may be released from predation or competition inside a fence • Game species, when the materials provided by fences for snares are outweighed by the protections they offer from human activities	• Species excluded from essential resources • Less marketable or charismatic species who are not management targets • Systems or functions that cannot occur within confined areas • Species susceptible to disease spread • Game species, when the materials provided by fences for snares outweighs their protections	Hotspots worldwide, with African reserves providing much of the scientific research
Infrastructure (e.g., roadside fencing)	• Open • Expensive • Designed for specific species or guilds • Paired with other management tools (e.g., underpasses)	• Target species in danger of injury or conflict because of infrastructure (e.g., wildlife–vehicle collisions) • Disturbance specialists and generalists that can incorporate fences into habitat • Invasive species requiring easy movement pathways	• Nontarget species or systems inhibited by fences more than infrastructure (e.g., migratory mammals)	Widespread along roads and development, especially in North America and Europe
Livestock or agricultural (e.g., pasture fencing)	• Closed • Impermeable to livestock • Easy and cheap to construct • Paired with range management and grazing	• High variation in livestock fence density makes winners and losers highly context dependent • Livestock • Invasive plants • Private landowners • Humans and wildlife adversely affected by human–wildlife conflict	• High variation in livestock fence density makes winners and losers highly context dependent • Native plant biodiversity • Vegetation growing along fence lines where trampling is common • Soil and plant productivity • Migratory terrestrial wildlife • Ground nesting birds • Smallholders or communal grazers reliant on open range	Common worldwide, extensive in rangelands
Political boundaries	• Open • Large scale • Expensive • Well maintained • Impermeable to many species	Generalists, disturbance specialists, and invasive species	• Large mobile wildlife species, and the systems in which they occur • Specialist species • Habitats occurring across borders • Wind propagated plants	Infrequent, at select boundaries only. Large in scale where they occur
Property boundaries	• Closed • Small scale • Low cost • Frequently maintained	• Generalists, disturbance specialists, and invasive species • Species benefitting from human shields • Sensitive habitats bordering development	• Large mobile wildlife species, and the systems in which they occur • Communities reliant on communal land or nondemarcated property • Wind propagated plants • Ground nesting birds	Common in already developed areas, but infrequent elsewhere. Increasingly common as property regimes shift globally
Invasive or pest	• Closed • Very large scale • Expensive • Impermeable to target invasive or pest species • Paired with aggressive management (e.g., eradications, restoration)	• Prey or competitors of excluded species • Native species or systems, where invasive species are effectively controlled	• Large mobile wildlife species, and the systems in which they occur • Livestock predators, when they are the "pests" being managed • Biodiversity, when large native predators are controlled	Infrequent, but large scale where present

sizes may fare worse inside reserves than outside of them because of the restricting effects of fences (Imbahale et al. 2008, Cole et al. 2012, Creel et al. 2013). An abundance of research has focused on large ungulates (as was discussed further in sections below) especially the disastrous effects of fences on migratory ungulates. Research on the loss of the blue wildebeest (*Connochaetes taurinus*) migration in Africa, for example, provided some of the earliest evidence regarding the ecological losers of a fenced world (Owens and Owens 1984). Even when mobile species are not blocked by fences, their ability and willingness to cross these features still has important effects on their habitat selection and access to resources. African elephants (*Loxodonta africana*), for example, avoid crossable fences and alter their subsequent areas of containment via their effects as ecosystem engineers (Vanak et al. 2010).

Even groups such as birds and reptiles, often assumed to be unaffected by fencing, may be parsed into winners and losers at the species level. Although many bird species readily ignore fences, ground nesting birds, such as members of the grouse genus (*Tetrao*), have high mortality rates because of fences, especially where fences blend in with background habitat features (Catt et al. 1994, Baines and Andrew 2003). Reptile species appear to have a special sensitivity to electric fences, because of the prolonged physical contact they may experience in crawling over or under fences, as opposed to flying, leaping, or digging beneath them (Ferronato et al. 2014).

It is impossible to build a fence that suits all species, and all traits, and therefore, as this review clearly shows, losers at the species level are inevitable regardless of fence goals and management practices.

Winners and losers at larger scales. It is important to point out the species-level bias in considering the impacts of fences: Most research included in our review examined the impact of fences on only individual species, and often the species for which the fence was constructed. There are far fewer examples of whole communities or ecosystems assessed as winners or losers because of fences. In this section, we summarize research on winners and losers at larger scales for different fence types. Even where conservation or restoration fences seemingly protect whole habitats, research still points to differential outcomes for constituent species (Imbahale et al. 2008, Cole et al. 2012, Creel et al. 2013). In addition, pathogens and parasites may spread more rapidly where species interactions are concentrated within reserves. In central Kenya, for example, smaller fenced reserves produced higher gastrointestinal parasite infection rates among impala (*Aepyceros melampus*; Ezenwa 2004).

For fences along roads, although target species may be protected from collisions with vehicles, these same fences likely produce losers at multiple scales. However, defining a whole ecosystem-level outcome in such cases is difficult, and we found no literature studying this. Conversely, several studies demonstrated the ways in which fences accompanying livestock management or subdivision of land created losers at large scales by changing nutrient flows, redistributing wildlife species, altering plant compositions, and creating habitat state shifts toward lower diversity systems with fewer native species (Maestas et al. 2003, Li et al. 2017).

Difficult tradeoffs are inherent in a fenced world, which creates winners and losers at different scales. Although most research studies winners at the species level, many impacts may be missed at larger scales. As fencing continues to rapidly proliferate, there is potential for a dangerous future in which fences simultaneously alter ecological processes at multiple scales, likely producing more losers than winners, and potentially resulting in ecosystem state shift or collapse (Hobbs et al. 2013, Løvschal et al. 2017, Heger et al. 2019). To avoid such a future, research must better uncover the ways in which fences affect nontarget species, the ways in which losers inevitably accompany winners, and the impacts of fences at multiple scales.

Moving forward: A typology of fence impacts to guide research

Identifying winners and losers in a fenced world shows how easy it is to overlook ecological effects of fences, especially when they may occur at multiple spatial or ecological scales. To help organize existing research and guide future researchers, we created a typology of fence impacts at different ecological scales on the basis of our systematic literature review. This typology reveals common types and mechanisms of impacts, even when the relevant spatial scales for species and systems may differ markedly. We categorized impacts by ecological scale and by 34 specific effect types as one framework for guiding future research, showing areas of emphasis and blind spots in existing fence research (table 2). Our review uncovered evidence for the effects of fences at every ecological scale of analysis, from the physiology and behavioral decisions of individual organisms to the functioning of entire ecosystems (table 2). However, our review also showed that research on fences has typically focused on a single ecological scale at a time, and often on a single species at a time. This means that the existing body of literature on fences, in spite of being large in number of studies, is idiosyncratic, narrowly focused, and as yet fails to provide suitable frameworks or guidelines to help interpret and compare findings. The typology we provide in the present article helps organize existing research, expose trends and gaps, and prompts questions for future researchers to pursue. Below, we discuss the trends we found at each scale of ecological analysis, as well as links across these scales.

Physiological and behavioral effects of fences. Some of the most abundant literature on the ecological effects of fences considers their behavioral and physiological effects on individuals. In particular, a robust literature on movement and crossing behaviors around fences shows the physiological and fitness risks that fences can impose as animals search for

Table 2. Typology of ecological impacts caused by fences and the number of studies examining each impact type.

Scale	Impact	Study count
Physiology	Injury or fitness change	27
	Energy expenditure change	21
	Physiology total	41
Behavior	Movement	140
	Crossing	123
	Foraging	64
	Migration disruption	36
	Predation or evasion strategy	29
	Social behavior	3
	Behavior total	207
Population	Distribution	103
	Altered population density	76
	Prevention of mortality	70
	Direct mortality	50
	Improved habitat suitability	49
	Indirect mortality	43
	Increased recruitment	43
	Population Isolation Reduced gene flow	38
	Reduced habitat suitability	29
	Reduced carrying capacity	14
	Demography	13
	Population total	258
Community	Community composition shift	92
	Species partitioning	52
	Multitrophic effects	40
	Altered interaction strength	37
	Inhibition of invasive species	12
	Increased disease susceptibility	10
	Facilitation of invasive species	8
	Reduced disease susceptibility	7
	Community total	150
Ecosystem	Ecosystem process alteration	65
	Habitat state change	35
	Erosion	15
	Habitat destruction	13
	Hydrological shifts	11
	Ecosystem total	92
Human	Human effects	107

breaks (Connolly et al. 2009), alter their optimal movement or foraging patterns (Vanak et al. 2010), and adopt novel crossing behaviors or are injured or killed in efforts to cross (Harrington and Conover 2006, Gates et al. 2011). Several studies have shown that mobile species constantly patrol fence boundaries seeking breaks, often finding them within hours. In New Zealand's Maungatautari Ecological Island, for example, a heavily fenced reserve that excludes invasive species, rats (*Rattus rattus*) and other small invasive mammals constantly patrolled the fence and typically identified fence breaks within 24 hours (Connolly et al. 2009).

Although the majority of these physiological and behavioral effects have been documented as directly affecting wildlife, plants and other nonwildlife species may also be affected. Indirect effects of fences on plants are also common. For example, domestic and wild herbivores preferentially move and feed alongside fence lines, resulting in increased trampling, changed growth patterns, and altered seed dispersal (Evans 1997, Grudzinski et al. 2016). Cumulatively, these behavioral changes in animals can alter recruitment and plant community composition. In the semiarid succulent thicket biome in South Africa, for example, contrast studies on either side of fence lines reveal changes in composition, litter production, and decomposition (Lechmere-Oertel et al. 2008). Restricting animal movements may also have important protective effects for plants and range-restricted species, with numerous studies showing the restorative effects fences provide when they prevent trampling or herbivory, especially of sensitive riparian habitats (Opperman and Merenlender 2000, Loo et al. 2009, Muller et al. 2016).

Population effects of fences. The effects of physiological and behavioral changes accumulate at larger scales to affect whole populations. For wildlife species, studies have shown fences alter movement and habitat selection patterns that alter population distributions (Chirima et al. 2012). Likewise, many plant species have been shown to accumulate along fences, especially along larger infrastructure fences such as sand and snow fences (Nordstrom et al. 2009, Loik et al. 2013). When migrations are critical to species survival, several high-profile studies have shown the catastrophic effects of impermeable fences that cross migration routes and the resulting population declines that follow, especially for wildebeest migrations in southern Africa (Owens and Owens 1984, Whyte and Joubert 1988). Similarly, where fences impede connectivity, genetic isolation or reduced gene flow may occur. A striking example showed that a planned US–Mexico border fence would dangerously restrict gene flow among desert bighorn sheep (*Ovis canadensis mexicana*), isolating populations across the border (Flesch et al. 2010). Demographic changes may also be detected if phenotypic differences across fence lines result in differential mortality or distribution within populations.

Community effects of fences. At larger scales, fences may have effects on species interactions and community composition, either directly or through the snowballing of smaller-scale changes described above. One study showed the potential of fences to alter community composition, demonstrating that African wild dogs (*Lycaon pictus*) in Botswana readily crossed a fence to find spatial refuge from competing lions (*Panthera leo*), which showed a reluctance to cross the fence's narrowly spaced wires (Cozzi et al. 2013). Several studies made clear that even when fences do not strictly partition species, they can still radically modify the strength of species interactions. For example, predator and prey behavior and distributions, altered by fences, may scale up to influence the outcome of this interaction. Altered interactions such as these also may facilitate or inhibit the success of invasive species. Although fences, by reputation, have been chosen to prevent the spread of such species, several papers identified their role in enabling the establishment of invasive species (Brown et al. 2006, Weller et al. 2011). In Australia, for example, restoration fences excluding livestock sped the invasion of the exotic aquatic grass *Glyceria maxima* (Loo et al. 2009). Interestingly, for some small species, fences may create habitat. Several studies show birds and insects using fences as nesting, lookout, feeding, or display sites (Lesinski 2000, Kamath et al. 2018), but further research is needed to understand the ways in which fences produce microhabitat variation.

Ecosystem effects of fences. The combination of the effects of fences mentioned in the present article, as well as numerous others identified in our review, can markedly alter entire ecosystems. At the ecosystem scale, however, it becomes especially difficult and unrealistic to view fences in total isolation. Fences work at multiple scales and have nuanced and differential effects both on their own and as part of systems of management or change. In Australia, for example, some of the world's longest fences have been paired with eradications of large predators such as dingoes (*Canis lupus dingo*) to protect livestock grazing areas. Although these enormous fences will have behavioral, population, and community level effects, some of their most important consequences are apparent as changes to entire ecosystems. Without dingoes, researchers have tracked a continental-scale mesopredator release that has altered biodiversity and habitats over enormous areas of Australia (Letnic et al. 2011).

As this example highlights, fences are important but overlooked components of many of the world's most powerful engines of anthropogenic change. It is difficult to isolate fence effects in part because fences so readily facilitate and may be confounded with other practices: livestock grazing, privatization and subdivision of land, road development, human settlement, and conservation. The cumulative effects at multiple ecological scales of a global network of fences only adds to the effects of these other drivers of ecosystem change. A number of fence-line contrast studies, which compare ecosystem characteristics on either side of a fence, show just how severe this change can be when fences enforce differential management (Todd and Hoffman 1999, Lechmere-Oertel et al. 2008, McGahey 2010).

We do not wish to argue that all fences are detrimental to individuals, species, communities, and ecosystems. Individual fences may serve powerful conservation or restoration functions and, in many cases, merit the high regard in which they are held as a management tool. However, our review makes clear that these roles can also obscure the cumulative, large-scale effects of a globally ubiquitous network of fences. Future research on the ecology of fences must strive to not consider these features in isolation, but to collect empirical data and theorize the multiple scales of impacts that fencing can create.

Socioecological effects of fencing. In addition to the ecological effects summarized above, a large number of studies have considered the effects of fences on humans (table 2). Fences are sometimes essential to society, and their social and economic roles force managers, policymakers, and land users to face deliberate tradeoffs between ecological and socioeconomic needs. An adequate treatment of this topic far exceeds the scope of this article. Nevertheless, in the present article, we briefly summarize some of the findings from this research.

Fences can directly affect human movements and behaviors in many of the same ways as was described above, as is forcibly demonstrated by border fences (McCallum et al. 2014, Linnell et al. 2016) and conservation fences (Spierenburg and Wels 2006, Chaminuka 2010). Fences also affect humans more indirectly, because they facilitate changes in the concentration and movements of livestock (Li WJ et al. 2007), the demarcation of boundaries and privatization of land (Xu et al. 2015, Evans and Adams 2016), and the concentration of power and access among large landowners or states (Albertson 2010, Knight and Cowling 2012, Hongslo 2015, Evans and Adams 2016). Importantly, these effects on society are not distinct from ecological effects. A clear example of this link is found when communities deprived of resource access by conservation fences use fence materials to construct snares that have devastating impacts on wildlife the fences were meant to protect (Dunham 2001, Lindsey et al. 2011). Even where fences may have beneficial effects, such as limiting human–wildlife conflict (Linhart et al. 1982, O'Connell-Rodwell et al. 2000, Honda and Iijima 2016), their permanent placement may amplify other ecological impacts over time on a dynamic landscape, creating long-term consequences for human inhabitants (Taylor and Martin 1987, McGahey 2010). These brief examples highlight both the significance and the complexity of socioecological effects of fences, and we emphasize the pressing need for its further inclusion in fence ecology.

Trends and gaps in fence ecology research

The typology we present above makes clear many important opportunities for future research, but other trends and gaps also became apparent in our review. The large number of studies we reviewed (446) belies a shallow and narrow understanding of the cumulative impacts of fences. The strong topical and geographical biases found in the published literature on fences mean that what is left to learn about fences far surpasses what is already known. It is likely that these trends reflect in part the identities and goals of fence researchers and not the actual proportional geographical and topical distribution of fence effects, and we discuss these trends in this light.

We call attention to five important sources of bias that characterize the literature on fences: a taxonomic bias (fence research has been focused on economically important game species, especially medium-size ungulates), a scale bias (disproportionately little attention in fence research has been paid to complex community and ecosystem-level processes), a geographic bias (fence research has primarily come from a few countries found in temperate regions with large rangelands), biases in the type of fence studied (much of our inference about the fences that stretch furthest—e.g., livestock fences—must be drawn from those that may be built quite differently—e.g., conservation fences), and biases in the relationship between study species and fence purpose (we know little about species for which fences were not designed).

Taxonomic biases. Large mammal species have received by far the most research attention of any taxon. More than half of the studies in our review considered mammals as their focal species (table 3). Within mammals, ungulates were the most common subcategory, with 124 of the 446 studies focused exclusively on ungulates of approximately 100 kilograms in mass, the largest such focal group within the studies reviewed. Some of the earliest studies that we reviewed considered how fences that were built to restrict the movements of domestic ungulates might have similar effects on wild ungulate movements (Spencer 1948, Bauer 1964, Tierson 1969, Messner and Dietz 1973). This question has continued to preoccupy research on fencing; some of the most cited (Owens and Owens 1984, Whyte and Joubert 1988) and most recent studies (Jakes et al. 2018) that we reviewed have focused on effects of fences on wildlife movements. Taken together with the abundance of research on movement and distribution of species (table 2), these results suggest that much of the research on fencing has demonstrated that fences that effectively control livestock movements and distributions have similar effects on large mammalian wildlife species. This focus and outcome are not surprising considering the economic importance of such species as game animals and their physiological similarity to livestock species for which many fences have been built. Nevertheless, the range of fence studies we examined suggested a disproportionate emphasis on medium-size ungulates that has come at a cost to our understanding of fence-induced impacts on other species (table 3). In short, a large quantity of our knowledge about the ecological effects of fences tells us that fences restrict the movement and distributions of medium-size ungulates.

Scale biases. Although research has uncovered a great deal about fences and large ungulates, complex ecological processes altered by fences have received far less research attention. The large number of studies cited as showing ecosystem effects in table 2 masks the considerable overlap in these research efforts: Most of these point to systemic recoveries in small plots when livestock are fenced out. Many important large-scale processes remain understudied. Some of the least studied topics in our review include hydrological effects, facilitation or inhibition of invasive species, changes in diseases susceptibility, changes in demography or carrying capacity, and alteration of social behaviors (table 2). These ecological processes are far removed from the purposes for which most fences have been built. Similarly, only 8% (37 of 446) of studies we reviewed considered responses of multiple focal species. The studies that did incorporate multiple focal taxa supported several decades of research in community ecology by indicating that single species effects can cascade to the communities in which they occur, and may even have continental-scale outcomes (Letnic et al. 2011). There are likely numerous impacts of fences yet to be discovered as a result of the scarce research on slow and complex ecological processes.

Geographical biases. Our review showed startling trends in the geographical distribution of studies (figure 3). Within the 446 studies we reviewed, research has been concentrated in only a few nations, with five countries (United States, Australia, South Africa, China, and Botswana) accounting for over 50% of the studies reviewed in the present article (supplemental table S3). The United States was the site of 93 of the reviewed studies, accounting for over 20% of the total volume. North America (121 studies) and Africa (106 studies) were the most studied continents, whereas South America (15) was the least. The tropics, where much of the world's biodiversity occurs and where some of the most rapid proliferation in the types of land uses typically accompanied by fences is taking place, are particularly depauperate in fence research (figure 3). It is likely that these regions host important and diverse fence impacts that are underreported or as yet undiscovered.

Major research themes dominate each continent, meaning that the topical knowledge available on fences often comes only from a particular geographic context (figure 4). For example, most of the fence research in Africa has focused on conservation fencing, and conversely, much of our knowledge on conservation fencing comes from Africa. The same is true for fences to reduce invasive species in Australia, and livestock fencing in Asia, although there is much research on livestock fencing from other continents as well. Infrastructure fencing, primarily focused around roads, comes almost entirely from North America and Europe. Diversifying both the topics and the geography in which fence research occurs is therefore a pressing need. Even more importantly, it is clear that vast parts of the world, including much of South America, have seen very little research conducted on the ecological effects of fencing (figure 3), meaning that many context-specific consequences of fencing likely remain to be discovered.

Biases in fence types studied. Important trends also occur in the type of fences that have been studied, and we categorized fences according to the purpose of their construction

Table 3. The number of fence studies as a function of primary focal taxon.

Taxon	Number of studies	Percentage of total studies
Mammals	247	55.4
Vegetation	71	15.9
Multiple taxa	37	8.3
Birds	29	6.5
Herpetofauna	20	4.5
Humans	19	4.3
Invertebrates	16	3.6
Fungi	2	0.4
Fish	1	0.2

(table S1). Conservation fencing has been the subject of greatest study, and has received disproportionate attention considering its rarity relative to other fence types. Although livestock fencing has been the subject of the second largest number of studies, it is likely the most common fence type throughout the world and, therefore, has proportionately few studies relative to its abundance. Each of these fence types is distinct, and drawing conclusions across types is therefore problematic. The effects of a tall, electrified conservation fence cannot fairly be applied to a short, two-strand livestock fence.

Livestock fences in particular merit much greater research given their ubiquity throughout the world. Compared with most other fence types, livestock fences are more permeable to many species. We also classified the permeability of fences to the study species, and our results show that the least permeable fence types were the most well studied, accounting for 40% of included studies, whereas semipermeable (23%) and fully permeable (19%) fences were considered less frequently (supplemental table S4). Interesting research has begun to characterize the effects of fence permeability on species (Cozzi et al. 2013), but much greater research is needed to go beyond the simple conclusion that fences restrict species for which they are impermeable.

Biases in research targets. In the present article, we offer a simple but dramatic finding: 64% (285 of 446) of the studies were focused exclusively on the effects of fencing on target species—that is, species for which a fence was built. Only 24% of the studies included both target and nontarget species, and in a mere 12% were nontargeted species studied exclusively. Some of the most profound effects of fencing happen to nontarget species and systems (Ferronato et al. 2014), even as research focuses heavily on testing whether fences have effects on the species for which they were built. This is perhaps the most glaring omission in all of fence research, and shows that research has most often reflected the goals and needs of fence builders, rather than ecosystem management or multispecies conservation. In short, there is a diversity of impacts of fences on nontarget species that remain unstudied and, therefore, unreported.

Research and policy recommendations

Our review suggests fence construction is proliferating rapidly worldwide, reorganizing ecosystems at multiple scales of ecological inference, and creating more ecological losers than winners. Nevertheless, fences have received surprisingly little consideration as drivers of global change, and fundamental questions about their ecological effects remain unanswered. We have presented frameworks and questions to help fortify a burgeoning subdiscipline of fence ecology, and future research in this domain will require interdisciplinary methods as well as links to related subdisciplines (e.g., road ecology, landscape ecology, novel ecosystems) to grapple with the complexities we have described. The dearth of data on the extent, topology, and physical characteristics of fences has also impeded efforts to quantify their impacts, and producing better catalogues of the features and locations of fences around the world should be a research priority.

Although this article has emphasized our limited understanding of the ecology of fences, fences have also been a blind spot in environmental policy (Hayward and Kerley 2009, Durant et al. 2015). Fence policy is currently dominated by aesthetic considerations (e.g., urban ordinances governing fence height and placement), but, as was shown throughout this review, fences merit thoughtful regulation as ecological disturbances.

We recommend two foci for policy action that follow from our research: fence design and placement and fence construction and removal. Beginning with fence design and placement, we point to the success of recent "wildlife-friendly" fencing initiatives. Through regulation of the physical design characteristics of fences, these efforts have meaningfully reduced the ecological impacts of fences for large and migratory wildlife species without sacrificing the utility of fences for human communities (Paige and Stevensville 2008, Jones et al. 2020). Building on these efforts, we advocate for comprehensive policies supporting fence designs that incorporate the ecological typologies we have presented and take a diversity of ecological winners and losers into consideration. Because fences have effects at multiple ecological scales, local policies on fence design and placement will be most effective when coordinated with regional policies. Careful regulation of the placement and structure of fences, as well as planned fence gaps (e.g., Dupuis-Desormeaux et al. 2016), can mitigate fence impacts on sensitive species, ecosystems, and processes, while still permitting fences to carry out practical functions.

In the long term, policy that limits fence construction or promotes fence removal is essential for limiting the rapidly increasing ecological impact of these structures. Fences are often constructed with little specificity regarding their ecological roles and goals, and short-term functions receive priority over long-term outcomes (Sun et al. 2020). Research

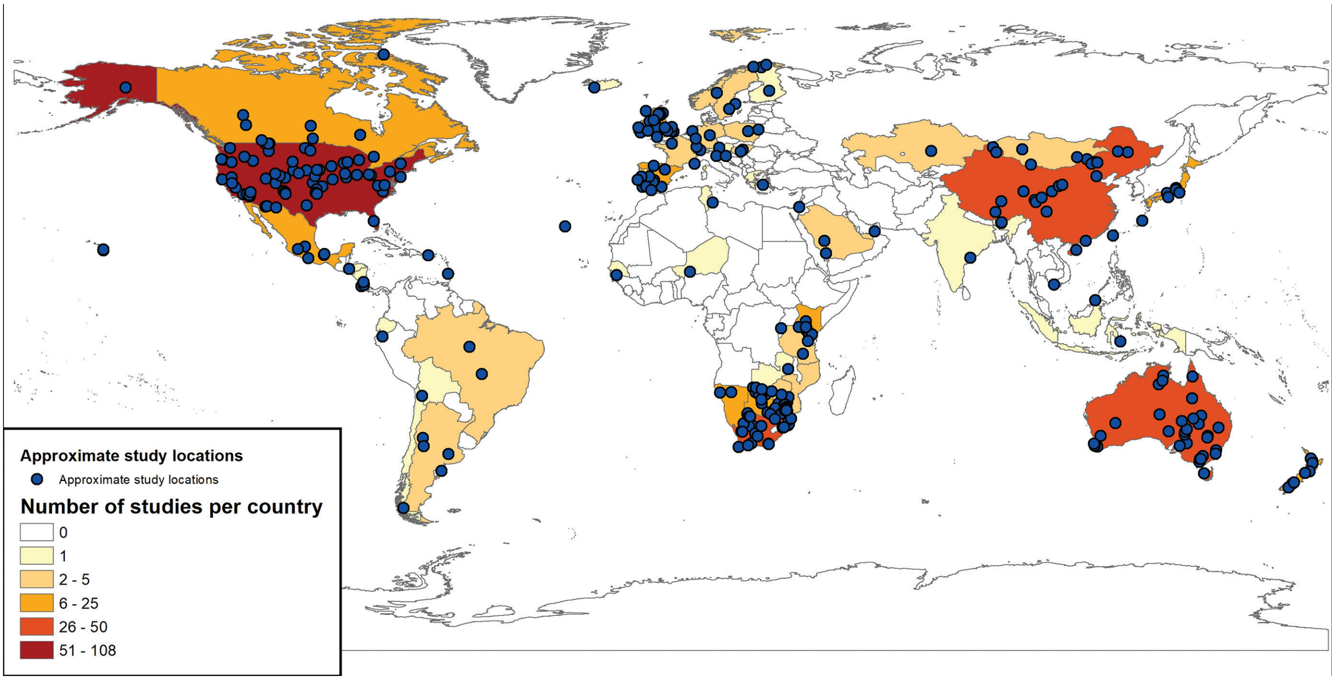

Figure 3. Study locations and countries where fence research has been conducted. Sixty countries have been home to research on the ecological effects of fences, but 38 of these have had only 1 such study. Five countries account for more than 50% of the studies reviewed in the present article.

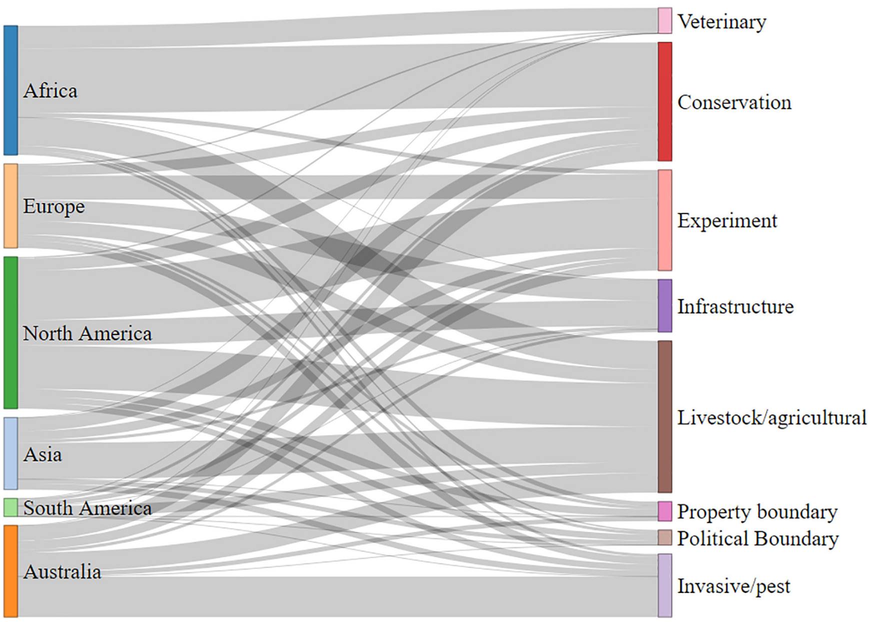

Figure 4. The type of fences studied in each continent. Several continents have a clearly dominant focal type of fence within their body of research. Likewise, several fence types have been primarily researched on single continents. Diversity in both the geography of research and the type of research conducted is a clear need for future efforts in fence ecology.

describing the full spectrum of ecological impacts of fences can provide a basis for policy that restricts fence construction or incentivizes fence-free areas. Such research-based regulations are common for other forms of linear infrastructure, but they remain rare for fencing.

Scientists have begun to consider the ecological merits of conservation fence removal (Boone and Hobbs 2004, Hoole and Berkes 2010, Woodroffe et al. 2014, Sun et al. 2020), and we recommend the expansion of fence removal programs to other fence types. Over time, the restoration of large tracts of fenceless land will benefit ecosystems and the services they deliver, while also providing important baselines for comparative research. Critically, any policies for fence construction and removal will require thoughtful management and coordination across stakeholder groups and jurisdictions to yield effective outcomes. Addressing the ecological benefits of reduced fencing, the services fences provide local communities and economies, and the connections between fences and political power demands a keen awareness of the relationship between fences and systems of governance within socioecological frameworks (Albertson 2010, Knight and Cowling 2012, Evans and Adams 2016, Weldemichel and Lein 2019). Ultimately, a robust field of fence ecology will be well positioned to provide the science to manage and mitigate one of humankind's most pervasive alterations of our planet.

Supplemental material

Supplemental data are available at *BIOSCI* online.

Acknowledgments

We thank Briana Abrahms, Kendall Calhoun, Eric Dougherty, Melissa Chapman, Kaitlyn Gaynor, Lynn Huntsinger, David Kurz, Arthur Middleton, Tristan Nunez, Katy Seto, Phoebe Parker-Shames, Mary Power, Lindsey Rich, Amy Van Scoyoc, and Lauren Withey for helpful input. WX was supported by the Smithsonian Predoctoral Fellowship for the duration of the project. CEW was supported by a National Science Foundation Graduate Research Fellowship for the duration of the project. ND was funded by the German Federal Ministry of Education and Research (grant no. BMBF 01LC1820A).

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