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CONCEPTS & THEORY

Coupled ecological and management connectivity across administrative boundaries in undeveloped landscapes

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Abstract. Human-induced ecological boundaries, or anthropogenic ecotones, may arise where administrative boundaries meet on undeveloped lands. Landscape-level ecological processes related to factors such as fire, invasive species, grazing, resource extraction, wildlife, and water may be affected due to unique management strategies adopted by each administrative unit. Over time, different management can result in discernible ecological differences (e.g., species composition or soil characteristics). Thus, fragmentation in the management landscape can correspond to ecological fragmentation. Different ecological patterns may emerge due to an increase in the number of management units in a region, or due to an increase in the number of different types of management units in the region. Temporal effects and collaboration history can also affect the emergence of ecotones. We use conceptual models to explore the relationship between these aspects of management fragmentation and the anthropogenic ecotones between management parcels. We then use examples of different management challenges to explore how anthropogenic ecotones can disrupt ecological flows. Our models suggest that cross-boundary collaboration that enhances management connectivity is likely essential to ecological connectivity in the face of environmental and social change.

Key words: administrative boundaries; ecotone; landscape heterogeneity; management mosaic; management trajectory; social-ecological systems.

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Introduction

Large undeveloped landscapes have important ecological and conservation value but are often historical, social, and political patchworks. Landscapes can be politically and administratively complex, with stakeholders, communities, or government entities at various levels managing for a diversity of purposes in the midst of changing conditions (e.g., Pykäläinen et al. 1999, Sato 2000, Koontz and Bodine 2008). Private land tracts are interspersed among public lands, even in large, undeveloped (i.e., without residential or urban communities) landscapes. This complexity results in management mosaics (sensu Epanchin-Niell et al. 2010), with adjacent ownerships or administrative units (hereafter "tracts") that may be managed for single or multiple uses, including resource extraction, recreation, and conservation. Moreover, larger jurisdictions of public or private land may be segmented so that different land uses and multiple tracts occur within a single ownership (e.g., a single forest district may contain roadless or wilderness tracts as well as resource extraction tracts). At multiple scales, therefore, management complexity overlies undeveloped landscapes.

Differences in traits may arise among the various patches in these management mosaics. We suggest that in some circumstances, these differences may result in fragmentation driven by the coupled system, in which a lack of management connectivity can disrupt ecological connectivity even within undeveloped landscapes. Land management decisions can shape ecosystem structure and function, influencing species assemblages, disturbance, and soils (e.g., Milchunas and Lauenroth 1993, Cherney 2011, Holcomb et al. 2011, Yaffee 2011, Peco et al. 2012, Kim et al. 2015). Ecological conditions can in turn affect manager decisions and collaborations by influencing resource availability, resilience to and extent of disturbance, and natural resource distributions (e.g., Epanchin-Niell et al. 2010, Burr 2013, Bodin 2017). Due to these feedbacks (Brunson 2012, Liu et al. 2016), administrative boundaries have the potential to become ecological boundaries, thus linking management connectivity and ecological connectivity. Differences arising among adjacent tracks may ultimately manifest as ecotones, or abrupt changes in ecological characteristics on either side of boundaries, even within undeveloped landscapes.

Here, we illustrate this phenomenon using observed patterns and example management challenges from the western USA as a focal region, but this cross-boundary fragmentation is relevant to undeveloped landscapes around the world (Wittemyer et al. 2008). For example, increased ecotourism activity resulted in deforestation of tracts adjacent to Kibale National Park in Uganda, creating patchy forest cover and sharp ecotones along administrative boundaries as a consequence of differing management trajectories (Naughton-Treves et al. 2011). By exploring how management and ecological connectivity interact and discussing how this phenomenon affects real-world contexts, we aim to shed light upon the form and function of those relationships. We discuss hypothesized mechanisms of anthropogenic ecotone development, and the shape and speed of trajectories emerging from those mechanisms. These baselines are essential for ecologists and practitioners to predict and quantify such ecotone patterns across a variety of systems and to consider how they impact management challenges.

Connectivity in the Management and Ecological Spheres

Dividing formerly continuous landscapes into different administrative units creates adjacent tracts of land that may be subject to different management histories, particularly if administrators differ in missions, mandates, and management resources. In the USA, such lands include private lands as well as Tribal, federal (primarily U.S. Forest Service, Bureau of Land Management, and National Park Service), state, county, and municipal lands. On one side of a boundary, management may prioritize conservation and cultural preservation, while an adjacent multi-use tract is managed for recreation, hunting, and water resources. Administrative boundaries can follow natural ecotones, such as cliffs, mountain ridges, and waterways. When they do not, however, management differences can lead to anthropogenic ecotones by producing mosaics of social and ecological characteristics on the landscape (Holcomb et al. 2011).

Both ecological and management connectivity can affect the flow of organisms, energy, materials, and information across administrative boundaries (Box 1). Ecological connectivity includes both biotic and abiotic flows: species movements (i.e., foraging, migration, and dispersal for native and non-native species) and gene flow among populations as well as the spread of fire or sediment and nutrient transport in waterways (e.g., O'Donnell et al. 2011, McRae et al. 2012, Cawson et al. 2013). Management connectivity includes flows of information and resources that enable active collaboration. Sharing of knowledge, ideas, expertise, tools, equipment, and personnel time makes possible joint decision-making and action (e.g., Snow 2001, Mills et al. 2014, Bodin et al. 2016). When administrative boundaries are barriers to such flows, they may produce ecological or management fragmentation (Box 1). This fragmentation may be a product both of increasing the mere number of boundaries or management units, as well as increasing the number of types of adjacent management units. Differences among tracts produced by fragmentation could feedback to further increase management fragmentation by reducing shared challenges and opportunities for collaboration between administrators (Fig. 1). In this way, administrative boundaries that create new ecological and management boundaries and thereby limit cooperation (Holcomb et al. 2011, Bodin 2017) carry ramifications for both society and ecology.

Box 1.
Definitions of key terms and concepts

Connectivity (ecological or management): the permeability of tract boundaries to ecological flows such as species movements and range expansions, gene flow, waterways, or spread of fire or to social flows such as information or resource exchange. We suggest that ecological and management connectivity are positively correlated with one another.
Cross-boundary cooperation: the implementation of management strategies that span property boundaries and can thus address landscape management challenges.
Ecotone: abrupt changes in ecological conditions on either side of a boundary. Conditions may be structural or functional; functional changes can alter ecosystem processes and differentially impact species and functional groups.
Fragmentation (ecological or management): the lack of permeability of tract boundaries to ecological flows such as species movements and range expansions, gene flow, waterways, or spread of fire or to social flows such as information or resource exchange. We suggest that ecological and management fragmentation are positively correlated with one another.
Management mosaic: a landscape composed of multiple management tracts under various administrations, where a tract is a management unit. We focus here on undeveloped landscapes.
Tract: a distinct ownership or management unit.

Social connectivity influences human institutions, well-being, information sharing, and decision-making. Jointly managing resources requires trust and connectedness between individuals across the management landscape (Pretty 2003, Barnes-Mauthe et al. 2015). Such connectedness is a key component of social capital, one of the community capitals that sustain livelihoods in resource-dependent communities (Flora and Flora 1993, Pretty 2003). For individuals, social connectivity can enhance feelings of well-being and make them less likely to abandon rural ways of life or sell to developers (Pretty and Ward 2001, Brunckhorst 2002, Pretty 2003). In addition, connectivity for land managers gives them access to information, public goods, and services which allow them to cooperatively address cross-boundary challenges and make decisions that support society as a whole (Pretty and Ward 2001, Pretty 2003). Similar management objectives across a management mosaic could increase management connectivity by elevating commonalities among individuals. This in turn may boost cross-boundary cooperation, information sharing, and decision-making.

Ecological connectivity can be described or measured in a variety of ways (Leitão et al. 2012), but is often examined across large landscapes that include anthropogenic barriers (Dickson et al. 2017). A stark transition between forest and grassland, for example, which emerges from distinct land management approaches can disrupt connectivity for some species across this boundary. The degree to which ecosystem fragmentation affects species or ecological processes will depend on scale and context. For example, a plant's distribution may be highly restricted by microsite soil chemistry, whereas a large carnivore may move regularly across a full and heterogeneous management mosaic. Sustaining wide-ranging species, native plant diversity, and resilience to disturbance frequently requires ecological connectivity (Damschen et al. 2006). At the same time, ecological connectivity can create favorable conditions, for example, for the spread of fire or invasive species if conditions are sufficiently homogeneous across a landscape.

Contiguous large landscapes are likely to retain necessary functions when both social and natural connectivity are maintained (Pretty and Smith 2004). Existing governmental structures typically

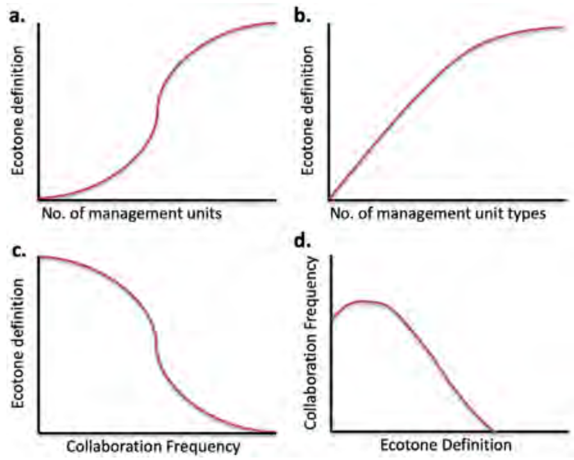

Fig. 1. Conceptual diagrams exploring the potential mechanisms underlying the hypothesized emergence of human-induced ecotones as a result of management fragmentation across a management mosaic. (a) The ecotone emerges as the number of management units increases. (b) When an increased number of units of different types are present, the resulting ecotone is more significant. (c) More frequent collaboration reduces ecotones. In a feedback cycle, (d) ecotone emergence is likely to encourage some types of collaboration, but increasing variation among administrative units hampers increased collaboration.

cannot address problems such as cross-boundary environmental degradation that occur at large scales and involve non-local influences (Dietz et al. 2003). Thus, strategies to address these challenges may involve dialogue to improve management connectivity across boundaries (Ostrom 1990, Berkes et al. 2006). Localized collaborative initiatives have existed for centuries to govern common-pool resources (Ostrom 1990). As cross-boundary issues have become more complex and non-local influences have grown, collaborative institutions may help sustain rural livelihoods and facilitate cooperation among private landowners or between private and public land managers (Schulte et al. 2008). When multiple government entities are involved, regulatory restrictions and conflicting agency missions increase the difficulty of these efforts (Bergmann and Bliss 2004, Beever et al. 2014). The amount of collaboration occurring across boundaries is likely to influence the emergence of anthropogenic ecotones at those boundaries.

Development of Anthropogenic Ecotones as a Result of Varying Management Trajectories

Ecological and management fragmentation rises as the landscape is divided into an increasing number of management units (Epanchin-Niell et al. 2010). An increased number of tracts can correlate with increased management fragmentation (i.e., reduced collaboration, cooperation, and communication across the management landscape) due simply to the enhanced number of players involved and thus enhanced transaction costs of collaboration (Heikkila and Gerlak 2005). Increasing the number of types of tracts can further deepen management fragmentation across the landscape because the mandates, missions, and objectives of managers become more variable. Management decisions and activities beneficial to some tracts may seem detrimental, low priority, or impossible to other managers.

These contrasting management conditions across boundaries overlie inherently complex ecological landscapes. Landscape ecologists describe broad land areas with regard to their spatial elements—for example, habitat patches, edges, matrix, corridors, and connectivity, evenness, flow resistance—and examine the processes that yield visible patterns in those elements (Turner and Gardner 2015). Importantly, even before the management mosaic is established, landscapes are inherently heterogeneous, and landscape ecology examines that heterogeneity and its effects. Our focus here on large landscapes divided by administrative boundaries thus mirrors the focus of landscape ecology. The socio-ecological landscape of our framework comprises overlapping spatial elements in both the administrative/ownership and ecological spheres.

Spatially, our framework applies to ownership boundaries and thus distinct patches, or tracts, with defined boundaries on the management landscape. However, a key challenge is differentiating when there is a mismatch between tract boundaries and natural, ecological heterogeneity to which organisms are adapted. When administrative boundaries follow real ecological boundaries (e.g., waterways, ridgelines, or canyon edges), changes in ecological and management traits should spatially coincide. Therefore, underlying heterogeneity can drive ecological differences between adjacent tracts that increase with distance from a boundary, even in the absence of management-derived differences. This gradient can also obscure the fragmentation effects of administrative boundaries described in our conceptual framework. Similarly, if habitat patches naturally turn over at fine spatial scales, ecotones arising as a result of differing management trajectories may be difficult to detect because inherent heterogeneity on the landscape is large. In this case, differences within patches may be larger than differences between patches. If, however, the resolution at which natural heterogeneity occurs is coarse, then ecotones generated by administrative boundaries may become more obvious because they impose changes across tract boundaries that do not reflect the underlying ecological matrix. At this scale, anthropogenic heterogeneity is inconsistent with ecological heterogeneity. Species and ecological communities are unlikely to be adapted to such new heterogeneity across the landscape, and natural habitat patches as well as the populations within them may become reduced in size or fragmented. As an example, greater sage-grouse (*Centrocercus urophasianus*) populations are significantly larger where human infrastructure density is low and native grasses dominate (Knick et al. 2013). Management guidelines recommend protecting a 32-km^2 area surrounding an active lek, or gathering of males in mating displays (Connelly et al. 2000). The more ownership fragmentation there is across sage-grouse habitat, the less likely it is that all jurisdictions will manage in such a way as to meet these criteria.

Conceptual Models: Mechanisms by Which Anthropogenic Ecotones may Emerge from Different Management Trajectories

Conceptually, there are several mechanisms we expect to shape the development of human-induced ecotones as a result of management boundaries. Here, we focus on four of these mechanisms: an increased number of management units within a landscape, an increased number of management types, temporal effects, and the role of deliberate collaboration.

The number of management units within a landscape

The existence of a higher number of management units within a given area has been associated with decreased recreation opportunities, declines in forest health, and negative impacts on local communities and local economies (Gobster and Rickenbach 2004). Large tracts can support homogeneous management strategies that produce continuous ecological traits such as road density, grazing intensity, and fire management. By contrast, landscapes divided among multiple tracts contain different management activities due to increasing complexity of communication and a greater number and frequency of management decision points. Ultimately, variation in landscape traits that arise from even small differences in management can act as anthropogenic ecotones—discontinuities in vegetation features, soil characteristics, disturbances, etc. (Fig. 1). The likelihood of such ecotones emerging, and their density on the landscape, should increase with an increasing number of managers across the social landscape. Because the driving mechanism is explicitly spatial, this increase might be expected only up to a certain point, beyond which subdivision of tracts in an undeveloped landscape is no longer feasible (Fig. 1a).

The number of management types within a landscape

Land tract management type can be defined by objectives and uses (e.g., resource extraction, grazing, recreation, conservation), mandates (e.g., preservation, multiple use), political hierarchy (e.g., federal, state, county), and intensity (active vs. passive management vs. wilderness). An increase in the number of management types should cause ecotones to arise even faster or be more distinct than an increase in the number of management units alone (Fig. 1b). For example, different management objectives could result in logging on one side of a boundary and forest restoration on the other, or grazing on one side of a boundary and hiking trails on the other. In other cases, these differences in management may be much more subtle: Different fire management regimes may lead, for example, to varying grass species assemblages or raptor nest densities on either side of a boundary. As with increasing the sheer number of units, an asymptote may eventually limit the emergence of ecotones across the landscape, because differences in management types are finite in number (Fig. 1b).

Temporal effects

Emergence of ecotones is likely to reflect an important temporal effect that may be difficult to predict. Small differences in management may result in pronounced ecotones when magnified over time: For example, a decision to thin fuels to prevent fire, or to carry out a prescribed burn, could preserve vegetation in one tract if a subsequent wildfire causes stand replacement on neighboring tracts. Similarly, differential management of livestock grazing can result in slow, cumulative changes in rangeland vegetation composition and soil structure over time (e.g., Lucas et al. 2004). In many parts of the western USA, a strong shift across landscapes over time from utilitarian to amenity ownership (e.g., hobby owners) is driving significant change in land use practices today. This change has the potential to result in unpredictable and varied patterns across administrative boundaries (Travis 2013). As an example, amenity owners in some cases have been shown to lack the knowledge or incentive to control invasive species (Epanchin-Niell et al. 2010). Temporal trajectories can add complexity when a single tract changes owners, management types, or management objectives repeatedly over time. Over the course of a few decades, such a single tract could be managed for extraction, recreation, conservation, and grazing. How the vegetation, disturbance regime, and biodiversity in a tract compare with neighboring tracts following such a varied history may be unpredictable.

The role of deliberate collaboration

Deliberate collaboration between adjacent tract owners or managers can be fundamental to ecotone development and evolution. If heterogeneous conditions on the landscape are desirable (e.g., timber extraction may be allowed in one tract whereas an adjacent protected area retains old growth forest to serve as a biodiversity refuge), collaboration could create or sharpen an ecotone. When natural flows and natural heterogeneity are preferred, collaboration can reduce the sharpness of ecotones, make them less likely to arise, or erase them over time (Fig. 1c). Collaborations can allow management strategies to span areas of multiple ownership. For example, partnerships formed to meet climate adaptation goals may extend the physical area and thus effectiveness of conservation management approaches (Monahan and Theobald 2018). Coordinated fire or invasive species management may likewise reduce ecological differences between tracts (Burr 2013; Fig. 1d). However, collaboration effects are also subject to important effects of time (Fig. 1d). Both the length of time of divergent management before a collaboration forms and the age of the collaboration itself may impact the stability of an ecotone. Collaboration carries costs so is more likely to develop when personal relationships have formed and also after an ecotone has caused concern (e.g., if fire or weed invasion risk has increased in a carefully-managed tract simply because it is adjacent to an unmanaged tract; Monahan and Theobald 2018; Fig. 1d). Collaboration may be more sensitive to differences in management type than simply the number of management units, since similar objectives may make collaboration more likely or more sustainable. Successful collaborations that blur distinct ecotones, however, may themselves wane as resources are diverted elsewhere (i.e., a mission-accomplished feedback). Weakened collaborations may then help reestablish the ecotone, leading to a cycle of decreasing and increasing collaboration.

Real-World Application: Socio-Ecological Fragmentation and Management Challenges

Habitat fragmentation is a well-known conservation issue, but understanding ecological and management drivers of fragmentation is of increasing conservation importance as cross-boundary challenges confront management mosaics. Habitat fragmentation is traditionally discussed in the context of wholesale land use/ land cover change, that is, the clearing of native vegetation to make way for housing, agriculture, golf courses, etc. Changing land cover in such cases is intentional, and it is easy to measure the extent of the change. Management differences arising from the mechanisms discussed here are less recognized as drivers of ecological fragmentation and may arise more slowly or subtly. Nevertheless, these ecotones have implications for emerging management challenges that cross administrative boundaries. Here, we explore the implications of management fragmentation across undeveloped lands by considering differences among tracts in three key management challenges: fire, biological invasions, and grazing.

Fire

Under ongoing climate and land cover changes, wildfires have the potential to burn increasingly large areas, within and across administrative boundaries (e.g., Ager et al. 2018). In fire-adapted systems, fire suppression leads to fuel accumulation and enhanced risk of large fires. In non-fire-adapted systems, drought or human introductions of flammable non-native species can lead to fires that damage native communities and threaten native species. Different administrative tracts are likely to exhibit different fire management histories, philosophies, resources, and decision-making effectiveness (e.g., Charnley et al. 2016), all of which may impact fuels and fire events. The historical importance of management decisions in the form of fire suppression in western forests is highlighted by large shifts in the fire record following Native American depopulation (Taylor et al. 2016). As another example, an analysis including historical data (1911–early 2000s) of over 22,000 trees spanning a significant management boundary (Stanislaus National Forest and Yosemite National Park) in the Sierra Nevada found that the most significant difference between management parcels was a decrease in large, live trees in the national forest relative to the national park, with fire suppression cited as the likely dominant driver of forest change (Collins et al. 2017). In a study of roadless areas, wilderness areas, and multi-use U.S. Forest Service sites, increased road density correlated with reduced fire extent because roads facilitated fire suppression (Narayanaraj and Wimberly 2012). Road density, in turn, was the result of varying histories of administrative designation and associated mandates; wilderness areas were managed for minimal human impact, roadless areas were managed for multi-use without construction of new roads, and USFS lands were managed for multi-use including road construction (Narayanaraj and Wimberly 2012). As a result, individual tracts exhibited fire regimes distinct from those of neighboring tracts.

The use of managed or prescribed burns could also generate ecotones. A landowner's controlled burn could result in contrasting adjacent tracts, one with reduced fuels density and the other with higher fuels density that nevertheless maintains high neighborhood-level fire risk (Fischer and Charnley 2012). In other cases, such a decision could motivate neighbors to do the same (i.e., a contagion effect; Saengawut et al. 2016). Using field data on vegetation, fire models, and agency interviews, researchers found that differences in management of fire and resources have generated abrupt changes in vegetation patterns and predicted fire behavior at the administrative boundary between Grand Canyon National Park and the adjacent Kaibab National Forest (Fig. 2a), but also learned that attention to cross-boundary challenges and environmental change had boosted recent communication between agencies, resulting in shared land management objectives (Holcomb et al. 2011).

Biological invasions

Management connectivity among tracts may also have important effects on biological invasions. Early response to invaders requires resources, and flexible, responsive action, and collaboration among administrators may be essential to meet these needs (Kark et al. 2015). Specific land management techniques can affect

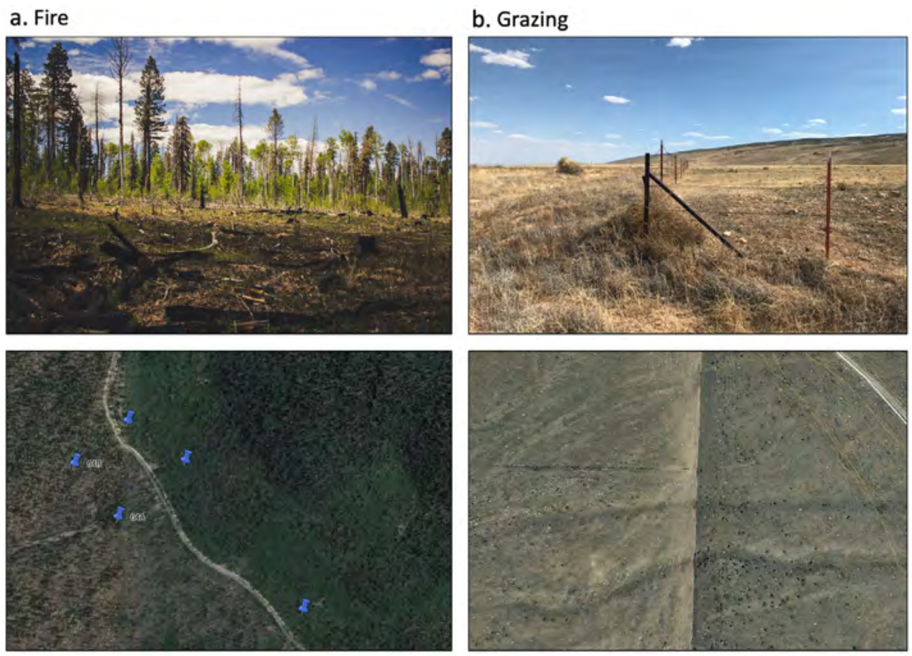

Fig. 2. Over time, different management practices can result in visible differences between undeveloped tracts across administrative boundaries. Illustrating this are paired plot-level (top) and associated images (bottom) of representative sites where administrative boundaries are demarcated by (a) presence of prescribed fire within a National Park and its absence within adjacent U.S. Forest Service Wilderness; and (b) different grazing stocking densities in adjacent private land tracts (photographs by M. Sample and C. Aslan; Google Earth v. 7.3.2.5776. Coconino County, Arizona, USA).

the establishment and spread rate of non-native species. The methods used to construct fuel breaks in California, for example, were found to significantly influence the abundance of non-native plant species: Fuel breaks constructed with bulldozers contained 28% non-native species cover compared with only 7% cover on fuel breaks constructed by other methods (Merriam et al. 2006). Buffelgrass (*Pennisetum ciliare*), a major invader in the southwestern USA, is promoted by both grazing (via hoofprint impressions for seed establishment) and roads (via vehicle dispersal and roadside disturbance; Stevens and Falk 2009). Administrative units allowing grazing and with high road density are therefore likely to exhibit more buffelgrass than units with no livestock grazing and/or low road densities. A survey of residents in the U.S. Southwest found that chemical control of invasives was more acceptable on multiple-use lands than on conservation lands, and mechanical control was less acceptable on public lands than private lands (Tidwell 2005). As with fire, a manager's invasive species control decisions may influence the effectiveness and likelihood of control efforts by neighbors (Epanchin-Niell et al. 2010). One quarter of ranchers surveyed in California reduced their investment in control efforts, considering them a waste of resources, if neighboring lands were sources of reinvasion. Divergent management objectives thus drove differences in control investment (Epanchin-Niell et al. 2010). These findings highlight the social complexity of the management mosaic and its capacity to influence invasive species' spread and densities.

Domestic livestock grazing

Livestock grazing is a primary land use for some administrative units (e.g., many private lands, leased public lands) and prohibited in others (e.g., most wilderness areas, some riparian tracts or sensitive areas, many parks, and conservation areas). Moving herds between summer pasture and winter ranges is one of the primary mechanisms of private to public land cooperation and ecological connectivity (Starrs 2018). Grazing heavily influences ecosystem characteristics lowering vegetation cover and diversity in many locations (Milchunas and Lauenroth 1993). Ceasing grazing elsewhere has increased fire frequency and intensity while decreasing soil nutrients (Peco et al. 2012). As with fire, grazing effects may depend on grazing intensity. Heavy grazing reduces litter accumulation and increases erosion risk (Schönbach et al. 2011). By contrast, moderate grazing boosts plant biodiversity in some systems (Schultz et al. 2011) and reduces densities of non-native invasive plants over larger spatial or temporal scales (Firn et al. 2013). Increasing the numbers of management tracts within an area may make positive grazing outcomes more difficult because grazers have uncertainty about long-term access to forage and thus may manage with less sustainability (Shapero et al. 2018). Side-by-side tracts under different grazing regimes may contain different species assemblages and vegetation structure and these differences may manifest abruptly at boundary fence lines (Fig. 2b).

Other contexts in which these processes are important

Management fragmentation across boundaries can introduce challenges across a variety of additional management contexts, including resource extraction, wildlife management, and water distribution. Approaches for meeting multiple land use objectives via cross-boundary planning and cooperation are needed to address these challenges (Sayer et al. 2013). For example, when tracts that allow timber harvest abut tracts that prohibit resource extraction, hydrology and soils may be expected to differ across the boundary (e.g., Boggs et al. 2015). Management targeted at particular wildlife species can have ecosystem level effects. For example, introduced bison in Grand Canyon National Park have damaged soils and native vegetation (Reimondo 2012), prompting park officials to consider bison culls. As bison shift their spatial distribution in response to park actions, impacts to vegetation and soil are likely to shift too (Reimondo 2012). Management of common-pool resources can be challenged by an increase in the number of tracts. For example, water users in the Bear River Basin voluntarily adopted collective water use limits in response to drought in the early 2000s (Endter-Wada et al. 2009); an increase in the number of neighbors makes collaboration in scenarios such as this more difficult by increasing transactional costs. Additionally, anthropogenic ecotones may be influential in the global trend of increasing emerging infectious diseases; a significant number of zoonotic diseases studied are associated with the presence of human-created ecotones (Despommier et al. 2006). As illustrated by these additional management arenas, linkages between ecological and management fragmentation have broad relevance to decision-making and the temporal trajectories of tracts.

Looking Forward: Breaking Management Barriers to Prepare for Novel Ecological Challenges

Coupled ecological and management fragmentation exacerbates problems posed by broad-scale environmental change. New challenges stemming from a changing climate, for example, may simultaneously affect multiple tracts in an area and/or necessitate species moving across several tracts (Kark et al. 2015). Such adaptive shifts may be hindered when ecological conditions change across boundaries as a result of different management trajectories, imposing local anthropogenic heterogeneity that further limits species. Habitat-specialist species may be particularly impacted, for example by fire management that impacts fire severity. The threatened Mexican spotted owl (*Strix occidentalis lucida*), declines in habitat occupancy following severe fire (Lommler 2019). Fuel management within a given tract then may impact owl colonization, and owners whose fuel management contributes to variation in fire severity may create a mosaic of owl habitats. Native fish populations with narrow habitat requirements may be impacted by fire with high enough severity to alter stream channel structure, water sediment loads, and nutrient availability (Dunham et al. 2003). The endangered red-cockaded woodpecker (*Leuconotopicus borealis*), by contrast, requires regular low-severity fire to retain its preferred overstory structure and will abandon habitats where fire has been suppressed for many years (Carlile 1995). For the endangered Fender's blue butterfly (*Plebejus icarioides fenderi*), both oviposition and caterpillar survival were higher a year after prescribed fire in prairie habitats (Warchola et al. 2015). As these examples demonstrate, management that results in anthropogenic shifts in fire regimes has the potential to fragment the habitats of conservation-dependent species.

To reverse management-driven fragmentation across undeveloped landscapes that span administrative boundaries, cross-boundary cooperation will be necessary (Kark et al. 2015). Neighbors share information and form social networks that directly influence land management decisions (Epanchin-Niell et al. 2010, Kittredge et al. 2013, Mattsson et al. 2018), which may help them respond to new challenges, particularly when effective responses depend on neighboring decisions (Wondolleck and Yaffee 2000). Although differences in management objectives may impede cooperation among private landowners, they are often more willing to cooperate with one another than with public agencies (Ferranto et al. 2013). This indicates the importance of encouraging more collaboration among private landowners or breaking down barriers to public-private cooperation, including unequal power or resources and divergent missions (Lachapelle et al. 2003, Bollig and Schwieger 2014). Durable relationships, regulatory frameworks, and a cultivation of trust can all spur public and private land managers to work together (Bergmann and Bliss 2004). Successful collaborations are often bottom-up and motivated by specific shared challenges, such as responses to pest outbreaks (Abrams et al. 2017), fires (Stasiewicz and Paveglio 2018), and wildlife conflicts (Weladji and Tchamba 2003). Stakeholder engagement processes also can advance communication and collaboration among stakeholders, building management connectivity, and perhaps reversing ecological and management divergence (e.g., Brody 2003, Keough and Blahna 2006, Rodriguez-Piñeros and Lewis 2013, Virapongse et al. 2016). Continued research into the formation, effectiveness (or lack thereof), and durability of such relationships may help lend insights that landowners and land managers can use to replicate successful responses to emerging problems.

Conclusions

Our synthesis identifies mechanisms and consequences of coupled ecological and management fragmentation across large landscapes. The various administrative units across a landscape are subject to diverse management trajectories as a result of differences in resources, mandates, and decision points. Anthropogenic ecotones may emerge from these divergent trajectories. The strength of such ecotones, and their rate of development, will be influenced by the number of administrative units in a region, the number of types of such units, and the frequency and degree of collaboration among managers. Managing connectivity in undeveloped lands will require an understanding of the complexity of socio-ecological systems (O'Farrell and Anderson 2010). To understand, model, and predict future ecological fragmentation caused by management fragmentation, interdisciplinary research can be applied to management mosaics across undeveloped landscapes worldwide.

Such understanding is fundamental to the sustainability of rural communities and ecosystem services within these lands, particularly under conditions of global environmental change (Cumming et al. 2015) that compel adjacent units to collaborate to achieve specific goals (Cumming et al. 2015, Liu et al. 2016, Schulte to Bühne et al. 2017, Stasiewicz and Paveglio 2018). Administrative boundaries can disrupt ecological and management connectivity across a region, impeding responses to cross-boundary management challenges (Cherney 2011, Yaffee 2011, Kim et al. 2015). Such disrupted connectivity interacts with boundary-spanning environmental changes, such as drought, fire regime change, biological invasions, and species' range shifts. As we document these changes and better understand the management mosaics they overlie, the scientific community will face a growing need to research and examine solutions and tools that can facilitate landscape-scale, cross-boundary management to preserve the functions and resilience of complex socio-ecological systems.

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