

Biotic and Abiotic Effects of Human Settlements in the Wildland–Urban Interface

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The wildland–urban interface (WUI) is the area in which human settlements adjoin or intermix with ecosystems. Although research on the WUI has been focused on wildfire risk to settlements, we argue here that there is a need to quantify the extent of areas in which human settlements interact with adjoining ecosystems, regardless of their ability to support fire spread. Besides wildfires, human settlements affect neighboring ecosystems through biotic processes, including exotic species introduction, wildlife subsidization, disease transfer, landcover conversion, fragmentation, and habitat loss. The effects of WUI settlements on ecosystems are two tiered, starting with habitat modification and fragmentation and progressing to various diffusion processes in which direct and indirect effects of anthropogenic activities spread into neighboring ecosystems at varying scales. New scientific, management, and policy tools are needed in order to better understand the WUI as a unique social–ecological zone and to mitigate negative consequences of its continued growth.

Keywords: fire, fragmentation, invasive species, wildland–urban interface, wildlife

Since the early days of human civilization, settlement has been one of the main footprints of humanity on Earth's terrestrial ecosystems. When human settlement occurs in natural or seminatural landscapes—excluding agricultural lands—it creates a wildland–urban interface (WUI). In this WUI, there are numerous interactions between human and natural processes, and these interactions occur both in the settled area and in the surrounding natural landscape (Radeloff et al. 2005a). Our goal here is to provide a synthesis of the patterns and processes of interactions between humans and their environment in the WUI, a widespread and growing coupled human and natural system (Liu et al. 2007) that is relatively poorly understood in its implications beyond wildfire.

There are many definitions of the WUI. Conceptually, the WUI is the area in which human settlements either abut or intermingle with natural or seminatural landscapes (Stewart et al. 2007). Accordingly, the WUI has two main components: the interface and the intermix WUI. The *interface* WUI is the area where human settlements (consisting of any number of houses, irrespective of whether they are urban, suburban, or rural) abut natural landscapes or wildland vegetation. These settlements are typically relatively dense and are often located along the edges of continuous swaths of uncultivated land (figure 1). The *intermix* WUI, in contrast, consists of sparser housing developments located amid the natural

landscape, where each house is surrounded by natural or seminatural lands (figure 1). In the intermix WUI, there are no clear boundaries among housing, roads, infrastructure, and wildlands; rather, it constitutes a zone.

Among all of the processes and interactions of humans and their environment in the WUI, wildland fire is the process that comes first to people's minds. In fact, the term *wildland–urban interface* has been used by the US federal government to define settled areas—and their surrounding wildland vegetation—that are prone to wildfire risk. The formal definition of the WUI by the US federal government is based on wildfire management and identifies WUI areas as those in which housing above a certain density threshold is in close proximity to wildland vegetation that can support wildfire spread (see interpretations by Radeloff et al. 2005a and Theobald and Romme 2007). Given that wildfires are responsible for numerous deaths and substantial economic losses due to the destruction of homes, most WUI research in the United States and Europe has been focused on human–wildfire interactions. Therefore, the term has become associated with the wildfire problem, but we argue here that the WUI is unique in many other ways and merits study and targeted management beyond wildfire issues.

Indeed, although wildfire is a key process in many WUI areas around the world, it is only one process among many, both abiotic and biotic, that have been altered by human

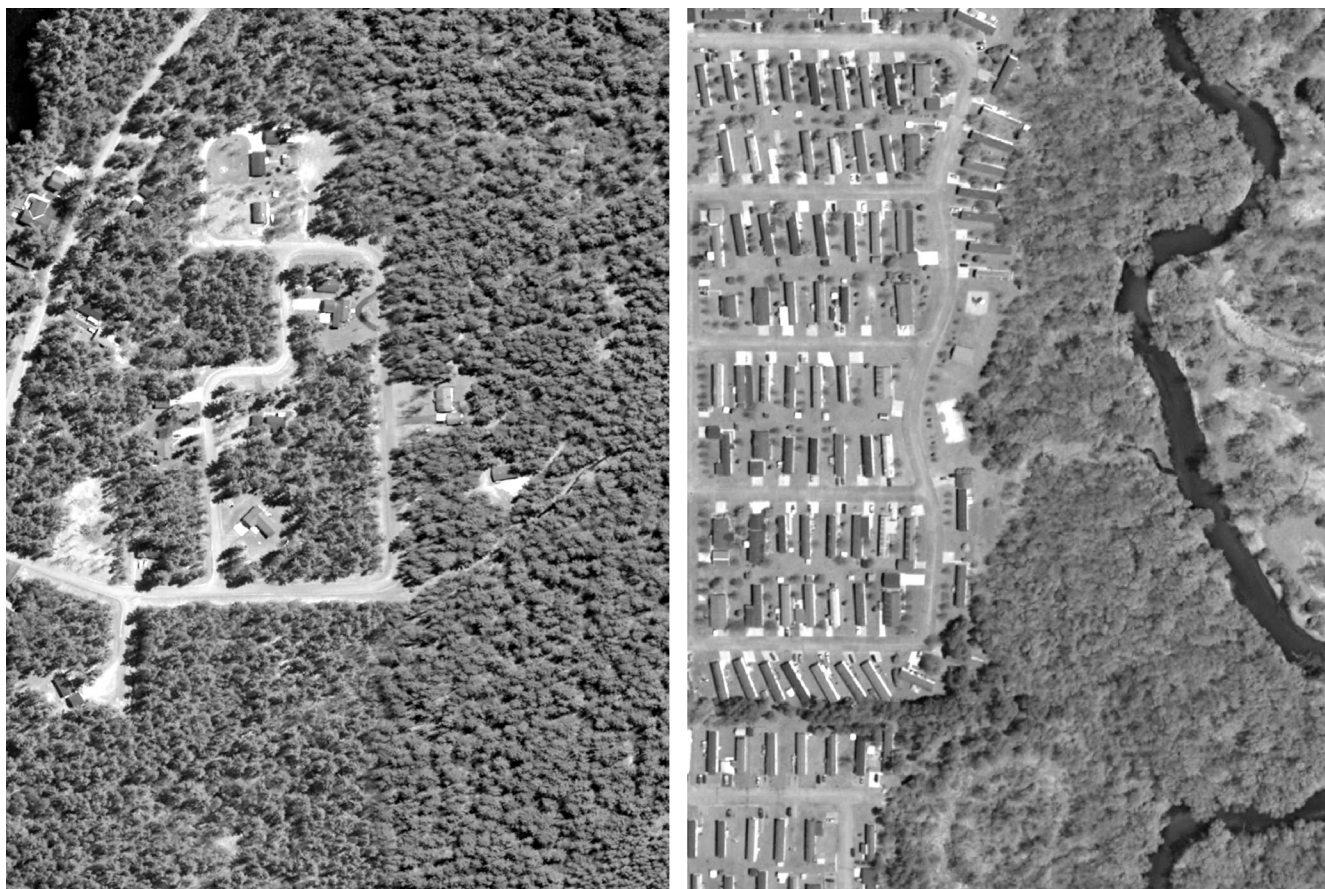


Figure 1. Examples of intermix (left) and interface (right) wildland–urban interface areas in central Wisconsin. Photographs: US National Agricultural Imagery Program.

activities and, in turn, affect human actions. Examining the WUI primarily in the context of wildfire fails to account for most of the effects that human settlements in the WUI impose on their surrounding wildlands, regardless of their fire regime. Whether fires are frequent—and whether fire regimes after settlement differ from presettlement regimes—ecosystems are affected by the WUI, and the area where human settlement adjoins or is intermingled with natural landscapes is much larger than the *fire WUI* that has been defined and mapped previously (Radeloff et al. 2005a). Hereafter, therefore, we expand the meaning of the term *WUI* to account for all settled areas—regardless of housing density—that are adjacent to or intermingle with natural or seminatural landscapes, irrespective of the wildfire context.

Therefore, our central argument here is that there is a need to quantify the extent of all areas where human settlements interact with natural and seminatural landscapes, regardless of their ability to support fire spread; to understand how ecosystem patterns and processes are altered in the WUI; and to adapt conservation and natural resource management to the unique setting that the WUI presents. To support this thesis, we briefly review and synthesize the current literature dealing with biotic and abiotic

interactions among human settlements, human activities, and the surrounding landscape, natural or seminatural, in and near the WUI. Our synthesis combines studies from distinct disciplines, including landscape ecology, conservation biology, animal behavior, plant ecology, and environmental science. Some of the processes that we review below have been extensively studied but not explicitly in the context of the WUI, and we include them here because of their relevance to the WUI context. The biotic interactions that we discuss include exotic species introduction and spread, wildlife subsidization, disease transfer, landcover conversion, fragmentation, and habitat loss, and the abiotic interactions that we discuss are wildfire ignition and spread (figure 2). Given that the WUI is inherently a spatial phenomenon, we conclude with a short section about mapping and quantifying the WUI and discuss the shortcomings and difficulties of mapping, in light of the multiple unique processes that occur within it.

Biotic invasions in the WUI

Human settlement in the WUI greatly facilitates the introduction of species—both native and exotic plants and, to lesser extent, animals—into the surrounding landscape.

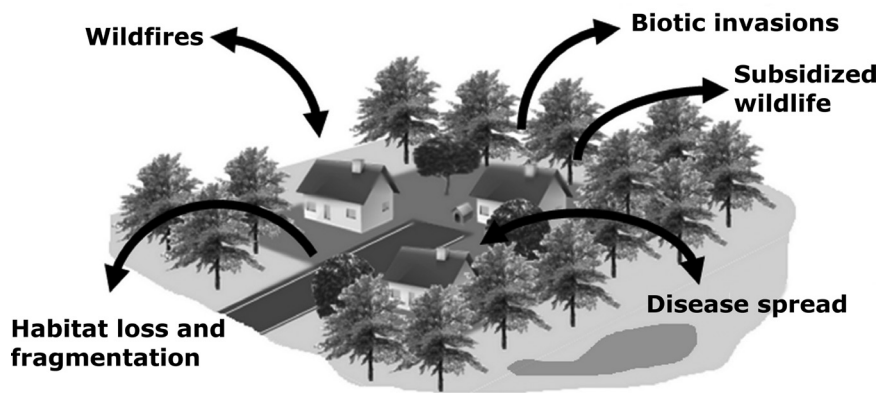


Figure 2. The biotic and abiotic processes associated with human settlements in the wildland–urban interface.

Human activity in the WUI facilitates plant introductions into natural areas by creating edges with higher light availability (Parendes and Jones 2000), which increases the propagule pressures from residential gardens (Raloff 2003, Sullivan et al. 2005, Gavier-Pizarro et al. 2010a), horticultural landscapes (Reichard and Hamilton 1997, Reichard and White 2001, Baskin 2002), and the dumping of garden waste (Batianoff and Franks 1998, Sullivan et al. 2005). Indeed, the vast majority of woody invasive species in the United States (82% of 235) were introduced for landscaping (Reichard and Hamilton 1997). Disturbances along the edge of development, which often cause abiotic changes, such as soil erosion (Rose and Fairweather 1997) and increased light availability (Parendes and Jones 2000), give competitive advantage to plant species that are better adapted to these conditions, and many of these are exotics (Davis 2003). Therefore, human settlement in the WUI, which is a unique case of habitat modification by humans, facilitates and supports exotic plant invasions and the spread of invasive natives through coupled processes: the formation of new edges, together with the availability of propagules (Alston and Richardson 2006). Propagules can then be dispersed by either natural vectors (e.g., wind or frugivorous birds) or anthropogenic vectors, such as garden waste dumping (Sullivan et al. 2005) or vehicles.

Although invasions are a major focus of current ecological research, in relatively few studies has the invasion process been examined in the WUI, but in those in which it has, strong associations were found. For example, exotic plant species richness decreases significantly with the distance from settlement edge in a small forest surrounded by WUI areas in the Table Mountain National Park, near Cape Town, South Africa (Alston and Richardson 2006). Some invasive species are more abundant closer to the settlement edge (e.g., *Ligustrum sinense* and *Quercus palustris*), and others are in areas that are more disturbed (e.g., *Acacia longifolia* and *Pinus* spp.). Similar relationships between exotic species richness and settlements occur at a local scale in New Zealand (Sullivan et al. 2005) and Wisconsin (Gavier-Pizarro

et al. 2010a) and at a regional scale in the United States (Gavier-Pizarro et al. 2010b). In coastal forests in northern New Zealand, exotic species richness decreases significantly with the distance from the nearest house and increases significantly when there are more houses within 250 meters (m) of forests (Sullivan et al. 2005). Moreover, exotic species richness in forests is moderately correlated with their richness in nearby settlements, and exotic species composition is similar in forests and their neighboring settlements. Finally, garden waste is found in 45% of the forest samples that are within 250 m of a house, and these waste dumps contain many

exotic species, which highlights the role of garden waste as a vector of exotic species spread into natural ecosystems (Sullivan et al. 2005). The association between houses and invasive species is robust across larger regions, too. In the northeastern United States, county-level richness of invasive exotic plant species was most strongly correlated with the WUI area, the area of low-density residential developments, and the increase in housing density from 1940 to 2000 (Gavier-Pizarro et al. 2010b). The WUI therefore represents the combination of the two main factors fostering invasive species: first, relatively high disturbance levels that create new habitats and, second, high propagule pressure, because landscaping provides seed sources that are easily dispersed by birds, wind, or garden waste.

The strong relationship between the WUI and invasive species spread is particularly fascinating because land-use legacies may exist, which suggests a lag time between the onset of invasion and its widespread manifestation, termed an *invasion debt*. In Wisconsin, current species richness and the percentage cover of four exotic species are more closely correlated with 1938 WUI settlement patterns than with present-day WUI patterns (Gavier-Pizarro 2009). Therefore, the distribution of invasive exotic species in the present landscapes is the outcome of WUI settlement spatial patterns about 70 years earlier, which determined the pattern of invasive species introductions. Such legacies exist because the spread of exotic species from WUI settlements into natural areas does not always begin immediately when exotic species are planted (Reichard and White 2001), either because of limited dispersal capabilities and low population growth rates at the onset of invasion or because of prevalent unsuitable habitat conditions. However, seemingly noninvasive exotic plants can become invasive long after their initial introduction (Reichard and White 2001). The exact mechanism that causes this change is often unknown (Raloff 2003), but it may be environmental change, evolution, or the introduction of a suitable pollinator or seed disperser (Reichard and White 2001). For example, three *Ficus* species in Florida that have been used for ornamental purposes for decades

and were unable to disperse naturally became highly invasive after the introduction of three exotic species of aganoid wasps, which are their sole pollinators in their native habitat (Frank et al. 1997). Therefore, the use of even seemingly harmless exotic species for gardening in WUI settlements may pose a risk for invasion, because the invasiveness of many species is unknown or hard to predict.

The studies described above suggest that to better understand the process of biotic invasions in the WUI (and to aid the development of management and policy actions that minimize invasions), further research must address three questions: (1) What is the spatial extent of invasions in WUI areas—that is, how far from settlements do invasions occur? (2) Which specific anthropogenic activities promote biotic invasions, and can they be reduced? (3) How do land-use legacies affect the invasion process?

Subsidized wildlife and interactions between domestic animals and wildlife

The WUI is also an area where processes such as wildlife behavior, predator–prey interactions, and—ultimately—food webs are altered by the subsidization of wildlife species. By subsidized species, we refer to three types of species that benefit from resource subsidies provided by human settlements: generalist wildlife species (e.g., jackals [*Canis aureus*], foxes [*Vulpes vulpes*]; Bino et al. 2010), synanthropic species (species associated with human habitats, such as purple martin [*Progne subis*]), and domesticated species (e.g., dogs [*Canis familiaris*] and cats [*Felis catus*]; Woods et al. 2003). Subsidized species are often generalists that can subsist on anthropogenic resources as well as on natural food sources (Boarman et al. 2006). The available resources may include food and water, nesting substrates, and insulation from predators and unfavorable weather conditions (Boarman et al. 2006). Subsidized species benefit from alternative food sources in and near the settlement, the availability of which limits their dependence on natural food sources. Alternative food sources can change food web dynamics by decoupling natural predator–prey interactions (Rodewald et al. 2011)—for example, when a drop in prey population does not lead to a drop in the predator population, because of supplemental food sources. Conversely, when access to anthropogenic food sources is lost, the survival rates of subsidized predators can drop sharply, which may eventually lead to the collapse of the entire population, as was shown in an experimental study of red foxes in Israel (Bino et al. 2010). In addition to alternative food sources, species may also have higher fecundity and increased population sizes in human settlements because of improved shelter and fewer predators (Boarman et al. 2006).

Prey populations are affected when predation rates increase because of artificially high densities of subsidized predators. Opportunistic subsidized predators, such as domestic cats, hunt even when prey populations are well below the level that can support native predator species, which leads to local extinctions of native prey species (Ross et al. 2013). In Great Britain, over a 5-month period, cats

brought home on average 11.3 prey items (2.26 per month), and mammals made up 69% of the prey items brought home, followed by birds (24%) (Woods et al. 2003).

In addition to direct predation, subsidized predators can affect native prey populations by forming *landscapes of fear* (Laundré et al. 2010), in which the risk of predation due to increased exposure to predators causes behavioral changes in the prey populations, including altered foraging and movement patterns. For example, in an agricultural area in Israel, where subsidized red fox populations flourish, gerbil (*Gerbillus* spp.) populations have lower activity levels and forage efficiency (Shapira et al. 2008). Similarly, the abundance of many rodent and bird species in a protected area near San Francisco, California, is lower in places frequently visited by domestic cats (Hawkins et al. 2004).

Another detrimental effect of subsidized domestic predators is competition with native predators. Artificially high domesticated predator populations compete with native predators for a finite amount of prey, which may subsequently reduce the populations of native predators. For example, Indian foxes (*Vulpes bengalensis*) alter their activity and foraging behavior in the presence of free-ranging domestic dogs (Vanak et al. 2009), and red foxes do so where subsidized golden jackals are present (Scheinin et al. 2006).

Domestic species may also be vectors of disease transmission to native wildlife populations, particularly where wildlife from urban and rural territories overlap. For example, free-ranging domestic dogs living in a rural area near Sengwa Wildlife Research Area, in Zimbabwe, are inefficient predators because of their small group size and body biomass, but they serve as prey for leopards (*Panthera pardus*), lions (*Panthera leo*), jackals (*Canis adustus* and *Canis mesomelas*), and spotted hyenas (*Crocuta crocuta*) (Butler et al. 2004). Because the subsidized canid population suffers high rates of rabies, the dogs' frequent predation by wild predators increases the transmission rates of canid diseases to wildlife species (Butler et al. 2004). Similarly, the incidence of canine parvovirus (CPV) is significantly higher among gray foxes (*Urocyon cinereoargenteus*) living in urban park areas than for those living in the rural park areas of Golden Gate National Recreation Area, near San Francisco, California (Riley et al. 2004), and foxes from rural park areas that cross into urban park areas are more likely to have CPV than are those that do not. In contrast, the incidence of feline calicivirus (FCV) is higher among bobcats (*Lynx rufus*) living in rural park areas than among those living in urban areas, and radio-collar tracking showed that bobcats with FCV traveled through park areas where domestic cats lived (Riley et al. 2004). Although the exact mechanics of transmission between species are not always fully understood, these examples highlight the risk of disease transmission that WUI areas pose.

Habitat loss and fragmentation

Habitat loss is the conversion of natural habitats into other landcover types (e.g., settlements, agriculture), often because

of human land use but sometimes because of natural processes, as well. *Landscape fragmentation* is the breakup of an intact, contiguous habitat into smaller fragments (Fahrig 2003). Both habitat loss and fragmentation have strong, detrimental effects on plant and animal species (Fahrig 2003). Habitat loss reduces the space available for plant and wildlife species, decreases wildlife population sizes, and can ultimately lead to extirpations and reduced species richness. Fragmentation limits the movement of organisms and materials across landscapes through introduced barriers of a different landcover type between formerly contiguous areas of the same landcover type (Edwards et al. 2004). Fragmentation can consequently disassemble metapopulations (Hanski and Ovaskainen 2000), thereby reducing the ability of plant and wildlife populations to regenerate after disturbances and demographic perturbations, because propagules or individuals from neighboring populations can no longer travel to the perturbed population. Furthermore, fragmentation greatly increases the amount of edge habitat, which can increase the susceptibility of remnant vegetation patches to disturbances and which fosters the introduction and spread of invasive species (Wiens 1992). In general, the process of replacing natural ecosystems with settlements often results in the deterioration of natural landscapes and in changes in biodiversity (McKinney 2002).

Conversion of natural landscapes into WUI areas by exurban development is associated with varying degrees of habitat loss and landscape fragmentation (Radeloff et al. 2005b, Irwin and Bockstael 2007), depending on the spatial configuration of the development and its intensity (Gonzales-Abraham et al. 2007). The biggest contribution to fragmentation in the WUI, however, is not from the conversion of natural landscapes into housing, which has a limited spatial extent overall but, rather, from the development of the road network that accompanies and often precedes human settlement in WUI areas (Forman and Alexander 1998, Hawbaker et al. 2006).

Interface and intermix developments may be associated with different levels of habitat loss and fragmentation. *Interface development*, in which houses are adjacent to wildland vegetation, is typically characterized by more dense housing than is *intermix development*, in which houses are interspersed within a matrix of natural vegetation. As a general approximation, interface development has a smaller impact on habitat fragmentation, because it is located at the edges of natural ecosystems and is typically more concentrated. In contrast, intermix development fragments habitat more, because the houses are located within a matrix of natural ecosystems. The ecological footprint associated with each intermix house is therefore larger than that of an interface house, because it is surrounded by natural ecosystems and requires, on average, a longer access road to connect with the main road network.

When considering the effects of human settlement on landscape fragmentation, it is important to recognize both direct and indirect effects (Theobald et al. 1997). The direct

effects stem from the conversion of natural habitat into built environments. Indirect fragmentation effects emerge from processes associated with human activities in wildlands near human settlements, such as vegetation thinning or clearing (to reduce fire risk), hiking (which affects wildlife species in various ways; Steven et al. 2011), hunting (hunting patterns are affected by housing patterns; Poudyal et al. 2008), and waste disposal (e.g., garden refuse, building materials). A building effect, or disturbance buffer, surrounds each dwelling (Theobald et al. 1997), such that the natural habitat is degraded even though it is not converted to a built environment. Houses therefore produce an indirect fragmentation effect greater than the direct effect imposed by the landcover conversion per se. Similarly, road networks are also characterized by a disturbance buffer, which increases their effect on the surrounding natural environment (Forman and Alexander 1998, Hawbaker et al. 2006). Roads can impede runoff and cause erosion, can be a source of chemical pollution (dust, heavy metals, nutrients, ozone, lead, and deicing salts), can promote light and sound pollution, can cause wildlife mortality, and can hinder faunal movements (Laurance et al. 2009).

Wildfires

Fires in the WUI pose great threats to human lives and property (Spyratos et al. 2007). However, WUI settlements also affect fire regimes. Where these areas constitute a sufficient amount of wildland fuel load, ignitions are likely, and the adjoining natural areas are at increased risk of wildfires (Syphard et al. 2007). In other words, WUI settlements raise the likelihood of wildfires, and wildfires are particularly threatening to people and properties in the WUI but also to natural ecosystems when their WUI-affected fire regimes differ from historical ones.

Compared with fires that are caused by natural ignitions—mostly lightning—anthropogenic fires are more frequent but tend to burn smaller areas, probably because of earlier detection and suppression, more roads to fragment vegetation, and less fuel within developed areas. However, anthropogenic ignitions are less common in places where it is feasible to allow fires to burn without suppression. In general, anthropogenic ignitions have a distinctive nonrandom spatial pattern: They occur near human infrastructure and activities, such as roads (Sturtevant and Cleland 2007, Syphard et al. 2008, Bar Massada et al. 2013) and houses (Bar Massada et al. 2013), and in areas of intermediate (Syphard et al. 2008) or higher housing and population densities (Sturtevant and Cleland 2007, Bar Massada et al. 2013).

Beyond the direct effects of wildfires on landscapes, an indirect effect of WUI fires is that people frequently modify the surrounding natural vegetation to reduce wildfire risk. Fuel treatments are often applied to vegetation adjacent to human settlements in order to reduce the vegetation's flammability and continuity—and, therefore, its potential to carry wildfire into settlements (Bevers et al. 2004)—and to improve access for firefighting efforts. Fuel treatments

include thinning to reduce the density of forest stands, removing understory vegetation, increasing the base height of the tree canopies to prevent surface fires from turning into crown fires, and removing vegetation completely—for example, when creating fuel breaks. Treatments to modify the vegetation may include prescribed fire, mechanical thinning, mastication, plowing with a bulldozer, applying herbicide, or a combination of these methods (Reinhardt et al. 2008). Treatments can extend from tens of meters to kilometers into the natural vegetation that surrounds WUI settlements (Schoennagel et al. 2009) and can cause significant changes in vegetated ecosystems. In the United States, for example, 1.5 million acres of wildland fuels were treated from 2004 to 2008 in and near WUI areas (Fitzsimmons 2009).

In addition to fuel treatments, fire suppression changes the vegetation near the WUI. Fire suppression has the opposite effect of fuel treatments on vegetation structure. Through the prevention of fires, more vegetative growth occurs, and both vegetation density and fuel loads can reach levels that are outside their historical range of variability (Minnich 1983, Hessburg and Agee 2003; but see Keeley et al. 1999 on the limitation of this paradigm in Mediterranean ecosystems of California). This is particularly problematic in landscapes that are fire dependent (Hessburg and Agee 2003). Fire suppression increases vegetative cover and, therefore, changes habitat characteristics, which, in turn, may alter species composition. The combination of extreme weather events with very high fuel loads due to consistent fire suppression can create extreme fire behavior that increases the risk to humans and wildlife alike (Hessburg and Agee 2003). Increased ignition frequencies due to growing human populations can also shorten the fire return interval below the range of natural variability, and, even in fire-adapted Mediterranean ecosystems, this can lead to the extirpation of native species by surpassing their resilience levels. For example, seeding species that need several years to mature to produce new seeds or resprouting species that exploit internal resource reservoirs to regenerate following fires may not be able to cope with very frequent fires. When this occurs, the result is a type conversion of the chaparral ecosystem into grasslands dominated by invasive species (Lippitt et al. 2012).

Mapping the WUI

The various processes by which human settlement in the WUI affects the surrounding natural landscapes pose complex challenges for reducing or mitigating their detrimental effects. Before any such management can be undertaken, it is necessary to map the WUI and quantify its spatial distribution at different scales, from local to global. Most existing methods for mapping the WUI are based on its fire-centric definition—that is, where human settlements are located near wildland fuels that can support wildfire spread and can, therefore, pose risks to humans (Radeloff et al. 2005a, Theobald and Romme 2007; see the supplementary materials). However, given the many different processes by which

human settlements and activities affect surrounding natural landscapes, single-focus WUI maps, such as those developed for wildfire management, are not sufficient to identify the full extent of the WUI. There is a need for a more general mapping approach, one that can account for settlement–wildland interfaces regardless of the vegetative characteristics of the wildland. A multifocal WUI mapping approach should encompass the spatial characteristics of the many biotic and abiotic processes that occur where human settlements are surrounded by wildlands. Unfortunately, inherent differences among these processes, their spatial characteristics, and their varying importance in different landscapes, coupled with the lack of sufficient data, make any single mapping approach incomplete. Alternatively, it may be more feasible to map each of these processes independently and then to combine the relevant individual maps into a multifocal map that denotes the footprint of any given settlement and the ecosystem in which it is embedded. Still, our limited understanding of fundamental ecological processes, such as the spread of invasive species and subsidized wildlife, make mapping even a single-focus WUI a challenge, and this constitutes a research area in which more work needs to be done. Our ability to map and to subsequently manage the WUI at scales larger than the local depends on our ability to increase the scientific understanding of biotic and abiotic processes through which people affect the natural environment around them.

Synthesis

Given the multitude of biotic and abiotic processes that occur in and near the WUI, at spatial scales from a few meters to several kilometers, we suggest that it is both meaningful and necessary to treat the WUI as a unique social–ecological zone. Traditionally, WUI areas have been viewed as transition zones between urban and wildland ecological systems. However, between 6% and 9% of the conterminous United States is composed of WUI areas (according to Theobald and Romme 2007 and Radeloff et al. 2005a, respectively; see figure 3; for a comparison, only 5% is water). The spatial extent of this area highlights its importance and prevalence at both regional and continental scales. Moreover, the current estimates for WUI areas are based on the constrained, fire-centric definition of the WUI, which is based on housing density above a given threshold coupled with sufficient prevalence of wildland fuels. A non-fire-centric WUI definition would incorporate all human settlements, irrespective of housing density, that co-occur with natural or seminatural landcover classes, regardless of the presence, density, and extent of wildland fuels. Such a definition of WUI would greatly expand the spatial extent of the WUI at the continental scale, further highlighting its importance as a unique area type that merits further study.

To treat the WUI as a distinctive social–ecological zone, we must integrate existing scientific, management, and policy tools to create new WUI-specific tools tailored to the unique characteristics of the WUI. The establishment

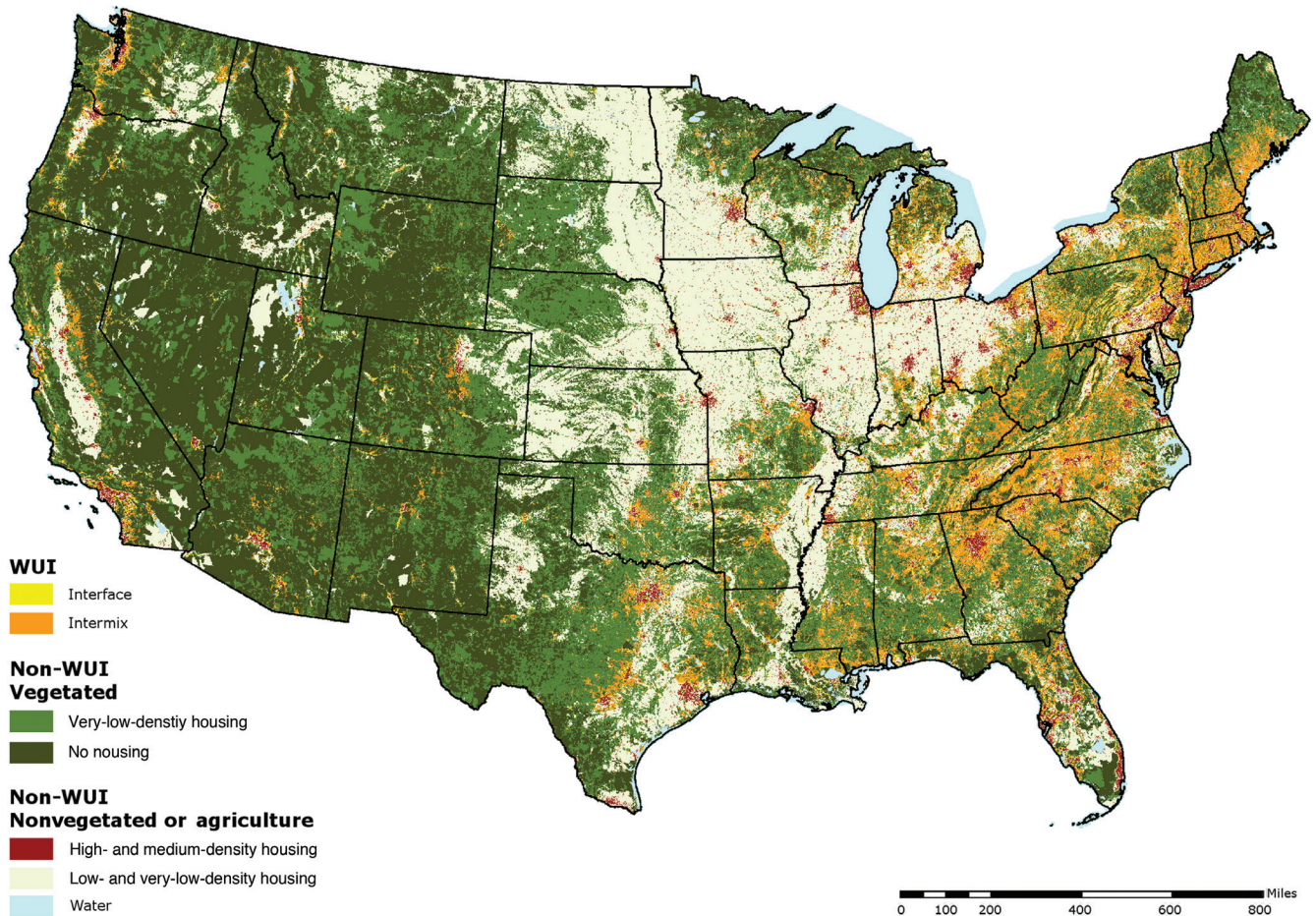


Figure 3. Wildland–urban interface (WUI) areas in the United States in 2010. The map is based on the zonal approach of Radeloff and colleagues (2005a).

of long-term ecological research stations in the WUI would facilitate ongoing ecological monitoring of WUI habitats and biotic processes, an important first step toward achieving these goals. Understanding unique WUI processes, such as fragmentation and wildfire initiation and spread, will require methods that can account for socioeconomic processes that drive WUI settlement patterns in the first place. Econometric models, spatial models of development, and fire risk models are promising frameworks for understanding the dynamics of WUI areas in the context of fire (Syphard et al. 2013) and can be extended and applied to a broader set of WUI-relevant ecological processes, such as habitat fragmentation and the spread of invasive species. For example, Martinuzzi and colleagues (2013) used a spatially explicit econometric model to predict future loss of significant habitat and biodiversity in the United States from an array of land-use factors—among them, urbanization. However, the complexity of the WUI makes it difficult to extrapolate findings to broader scales, because specific ecological processes associated with WUI settlements vary with development type and density and with the characteristics of the vegetation, topography, and climate. Biotic processes,

such as invasions and wildlife subsidization, differ according to the pool of local species and whether environmental conditions support additional species or altered food webs. Similarly, the magnitude of the negative outcomes of habitat loss and fragmentation depend on the characteristics of species that are exposed to these processes, and these are known to vary among regions as well. Therefore, both WUI mapping approaches and context-specific studies of WUI processes must account for such differences.

Conclusions

The WUI is the unique social–ecological zone in which human settlements abut or intermingle with natural or seminatural ecosystems, and it is a friction area in which multiple biotic and abiotic processes are affected or even driven by anthropogenic activities. Combining the processes that we have discussed, we suggest that the development of houses in the WUI has a cumulative effect on the surrounding natural ecosystem and its wildlife. First, WUI settlement causes habitat loss, which reduces the area available for wildlife and abiotic ecosystem processes and fragments habitats, therefore altering the flow of materials and organisms across

the landscape and decreasing its resilience to disturbances. Second, WUI development increases the magnitude of the human–natural interface and, consequently, promotes diffusion processes, such as the introduction and spread of invasive species, wildfire ignitions, and pollutants from settlements and roads into the surrounding landscape. These processes can have pervasive effects on human lives and property, as well as on plants, wildlife, and ecosystems.

Worldwide, humans are increasingly building houses in natural and seminatural ecosystems, and this means that a further increase can be expected in the coming decades in the extent of the WUI and in the magnitude of the detrimental processes associated with it. Therefore, we need new scientific, management, and policy tools that can help managers reduce the negative effects of settlement footprints in order to limit and mitigate the impacts of WUI settlements on the Earth's ecosystems.

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Supplemental material

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References cited

Alston KP, Richardson DM. 2006. The roles of habitat features, disturbance, and distance from putative source populations in structuring alien plant invasions at the urban/wildland interface on the Cape Peninsula, South Africa. *Biological Conservation* 132: 183–198.

Bar Massada A, Syphard AD, Stewart SI, Radeloff VC. 2013. Wildfire ignition distribution modeling: A comparative study in the Huron-Manistee National Forest, Michigan, USA. *International Journal of Wildland Fire* 22: 174–183.

Baskin Y. 2002. The greening of horticulture: New codes of conduct aim to curb plant invasions. *BioScience* 52: 464–471.

Batianoff GN, Franks AJ. 1998. Environmental weed invasions on south-east Queensland foredunes. *Proceedings of the Royal Society of Queensland* 107: 15–34.

Bevers M, Omi PN, Hof J. 2004. Random location of fuel treatments in wildland community interfaces: A percolation approach. *Canadian Journal of Forest Research* 34: 164–173.

Bino G, Dolev A, Yosha D, Guter A, King R, Saltz D, Kark S. 2010. Abrupt spatial and numerical responses of overabundant foxes to a reduction in anthropogenic resources. *Journal of Applied Ecology* 47: 1262–1271.

Boarman WI, Patten MA, Camp RJ, Collis SJ. 2006. Ecology of a population of subsidized predators: Common ravens in the central Mojave Desert, California. *Journal of Arid Environments* 67: 248–261.

Butler JRA, du Toit JT, Bingham J. 2004. Free-ranging domestic dogs (*Canis familiaris*) as predators and prey in rural Zimbabwe: Threats of competition and disease to large wild carnivores. *Biological Conservation* 115: 369–378.

Davis MA. 2003. Biotic globalization: Does competition from introduced species threaten biodiversity? *BioScience* 53: 481–489.

Edwards T, Schwalbe CR, Swann DE, Goldberg CS. 2004. Implications of anthropogenic landscape change on inter-population movements of the desert tortoise (*Gopherus agassizii*). *Conservation Genetics* 5: 485–499.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34: 487–515.

Fitzsimmons A. 2009. National Fire Plan fuels treatments target the wildland–urban interface in the western United States. *Proceedings of the National Academy of Sciences* 106: E87.

Forman RTT, Alexander LE. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics* 29: 207–231.

Frank JH, McCoy ED, Hall HG, O'Meara GF, Tschinkel WR. 1997. Immigration and introduction of insects. Pages 75–99 in Simberloff D, Schmitz DC, Brown TC, eds. *Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida*. Island Press.

Gavier-Pizarro GI. 2009. Understanding the Relationship between Housing and Exotic Plant Invasions. PhD dissertation. University of Wisconsin–Madison.

Gavier-Pizarro GI, Radeloff VC, Stewart SI, Huebner CD, Keuler NS. 2010a. Rural housing is related to plant invasions in forests of southern Wisconsin, USA. *Landscape Ecology* 25: 1505–1518.

———. 2010b. Housing is positively associated with invasive exotic plant species richness in New England, USA. *Ecological Applications* 20: 1913–1925.

Gonzalez-Abraham CE, Radeloff VC, Hammer RB, Hawbaker TJ, Stewart SI, Clayton MK. 2007. Building patterns and landscape fragmentation in northern Wisconsin, USA. *Landscape Ecology* 22: 217–230.

Hanski I, Ovaskainen O. 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404: 755–758.

Hawbaker TJ, Radeloff VC, Clayton MK, Hammer RB, Gonzalez-Abraham CE. 2006. Road development, housing growth and landscape fragmentation in northern Wisconsin: 1937–1999. *Ecological Applications* 16: 1222–1237.

Hawkins CC, Grant WE, Longnecker MT. 2004. Effect of house cats, being fed in parks, on California birds and rodents. Pages 164–170 in Shaw WW, Harris LK, Vandruff L, eds. *Proceedings of the 4th International Urban Wildlife Symposium*. School of Natural Resources, College of Agriculture and Life Science, University of Arizona.

Hessburg PF, Agee JK. 2003. An environmental narrative of inland north-west United States Forests 1800–2000. *Forest Ecology and Management* 178: 23–59.

Irwin EG, Bockstael NE. 2007. The evolution of urban sprawl: Evidence of spatial heterogeneity and increasing land fragmentation. *Proceedings of the National Academy of Sciences* 104: 20672–20677.

Keeley JE, Fotheringham CJ, Morais M. 1999. Reexamining fire suppression impacts on brushland fire regimes. *Science* 284: 1829–1832.

Laundré JW, Hernández L, Ripple WJ. 2010. The landscape of fear: Ecological implications of being afraid. *Open Journal of Ecology* 3: 1–7.

Laurance WF, Goosem M, Laurance SGW. 2009. Impacts of roads and linear clearings on tropical forests. *Trends in Ecology and Evolution* 24: 659–669.

Lippitt CL, Stow DA, O'Leary JE, Franklin J. 2012. Influence of short-interval fire occurrence on post-fire recovery of fire-prone shrublands in California, USA. *International Journal of Wildland Fire* 22: 184–193.

Liu J, et al. 2007. Complexity of coupled human and natural systems. *Science* 317: 1513–1516.

Martinuzzi S, Radeloff VC, Higgins JV, Helmers DP, Plantinga AJ, Lewis DJ. 2013. Key areas for conserving United States' biodiversity likely threatened by future land use change. *Ecosphere* 4 (art. 58).

McKinney ML. 2002. Urbanization, biodiversity, and conservation. *BioScience* 52: 883–890.

Minnich RA. 1983. Fire mosaics in Southern California and Northern Baja California. *Science* 219: 1287–1294.

Parendes LA, Jones JA. 2000. Role of light availability and dispersal in exotic plant invasion along roads and streams in the H.J. Andrews Experimental Forest, Oregon. *Conservation Biology* 14: 64–75.

- Poudyal NC, Cho S, Hodges DG. 2008. Effect of urban sprawl on hunting participation in the southeastern US. *Southern Journal of Applied Forestry* 32: 134–138.
- Radeloff VC, Hammer RB, Stewart SI, Fried JS, Holcomb SS, McKeefry AJ. 2005a. The wildland–urban interface in the United States. *Ecological Applications* 15: 799–805.
- Radeloff VC, Hammer RB, Stewart SI. 2005b. Rural and suburban sprawl in the U.S. Midwest from 1940 to 2000 and its relation to forest fragmentation. *Conservation Biology* 19: 793–805.
- Raloff J. 2003. Cultivating weeds: Is your yard a menace to parks and wild lands? *Science News* 163: 232–233.
- Reichard SH, Hamilton CW. 1997. Predicting invasions of woody plants introduced into North America. *Conservation Biology* 11: 193–203.
- Reichard SH, White P. 2001. Horticulture as a pathway of invasive plant introductions in the United States. *BioScience* 51: 103–113.
- Reinhardt ED, Keane RE, Calkin DE, Cohen JD. 2008. Objectives and considerations for wildland fuel treatment in forested ecosystems of the interior western United States. *Forest Ecology and Management* 256: 1997–2006.
- Riley SPD, Foley J, Chomel B. 2004. Exposure to feline and canine pathogens in bobcats and gray foxes in urban and rural zones on a national park in California. *Journal of Wildlife Diseases* 40: 11–22.
- Rodewald AD, Kearns LJ, Shustack DP. 2011. Anthropogenic resource subsidies decouple predator–prey relationships. *Ecological Applications* 21: 936–943.
- Rose S, Fairweather PG. 1997. Changes in floristic composition of urban bushland invaded by *Pittosporum undulatum* in Northern Sydney, Australia. *Australian Journal of Botany* 45: 123–149.
- Ross SR, Will T, Marra PP. 2013. The impact of free-ranging domestic cats on wildlife of the United States. *Nature Communications* 4 (art. 1396).
- Scheinin S, Yom-Tov Y, Motro U, Geffen E. 2006. Behavioural responses of red foxes to an increase in the presence of golden jackals: A field experiment. *Animal Behaviour* 71: 577–584.
- Schoennagel T, Nelson CR, Theobald DM, Carnwath GC, Chapman TB. 2009. Implementation of National Fire Plan treatments near the wildland–urban interface in the western United States. *Proceedings of the National Academy of Sciences* 106: 10706–10711.
- Shapira I, Sultan H, Shanas U. 2008. Agricultural farming alters predator–prey interactions in nearby natural habitats. *Animal Conservation* 11: 1–8.
- Spyratos V, Bourgeron PS, Ghil M. 2007. Development at the wildland–urban interface and the mitigation of forest–fire risk. *Proceedings of the National Academy of Sciences* 104: 14272–14276.
- Steven R, Pickering C, Castley JG. 2011. A review of the impacts of nature based recreation on birds. *Journal of Environmental Management* 92: 2287–2294.
- Stewart SI, Radeloff VC, Hammer RB, Hawbaker TJ. 2007. Defining the wildland urban interface. *Journal of Forestry* 105: 201–207.
- Sturtevant BR, Cleland DT. 2007. Human and biophysical factors influencing modern fire disturbance in northern Wisconsin. *International Journal of Wildland Fire* 16: 398–413.
- Sullivan JJ, Timmins SM, Williams PA. 2005. Movement of exotic plants into coastal native forests from gardens in northern New Zealand. *New Zealand Journal of Ecology* 29: 1–10.
- Syphard AD, Radeloff VC, Keely JE, Hawbaker TJ, Clayton MK, Stewart SI, Hammer RB. 2007. Human influence on California fire regimes. *Ecological Applications* 17: 1388–1402.
- Syphard AD, Radeloff VC, Keuler NS, Taylor RS, Hawbaker TJ, Stewart SI, Clayton MK. 2008. Predicting spatial patterns of fire on a southern California landscape. *International Journal of Wildland Fire* 17: 602–613.
- Syphard AD, Bar Massada A, Butsic V, Keeley JE. 2013. Land use planning and wildfire: Development policies influence future probability of housing loss. *PLOS ONE* 8 (art. e71708).
- Theobald DM, Romme WH. 2007. Expansion of the US wildland–urban interface. *Landscape and Urban Planning* 83: 340–354.
- Theobald DM, Miller JR, Hobbs NT. 1997. Estimating the cumulative effects of development on wildlife habitat. *Landscape and Urban Planning* 39: 25–36.
- Vanak AT, Thaker M, Gompper ME. 2009. Experimental examination of behavioural interactions between free-ranging wild and domestic canids. *Behavioral Ecology and Sociobiology* 64: 279–287.
- Wiens JA. 1992. Ecological flows across landscape boundaries: A conceptual overview. Pages 217–235 in di Castri F, Hansen AJ, eds. *Landscape Boundaries*. Ecological Studies, vol. 92. Springer.
- Woods M, McDonald RA, Harris S. 2003. Predation of wildlife by domestic cats *Felis catus* in Great Britain. *Mammal Review* 33: 174–188.

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