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Extent of fragmentation of coarse-scale habitats in and around U.S. National Parks

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ABSTRACT

U.S. National Park Service land managers face a variety of challenges to preserving the biodiversity in their parks. A principle challenge is to minimize the impacts of surrounding land use on park condition and biodiversity. In the absence of ideal sets of data and models, the present study develops methods and results that demonstrate a coarse-filter approach to understanding the effects of land use change on habitat types for four pilot study-areas. The area of analysis for each park is defined by a protected-area-centered-ecosystem. Habitat types were defined by biophysical factors assumed to represent the distribution of vegetation communities as they may have existed prior to European settlement. Present-day land use was overlaid on historical habitat and change in area and pattern was quantified for private and public lands separately. Results suggest that patterns of development are affecting study-areas differently. Therefore, the conservation challenges faced by each study-area are distinct to their landscape contexts. For some parks, the primary challenge is to work towards maintaining ecosystem condition in its present or near-present state while paying particular attention to habitats that are underrepresented on public lands. For other parks, the challenge is to address spatially aggregated land use that is affecting only a few habitat types. For still other parks, the challenge is to maintain connectivity with a regional network of protected lands and to undertake restoration projects where feasible. The present methods and results help to focus conservation attention on habitats that have been most impacted by land use change.

1. Introduction

Parks and protected-areas (PAs) represent a cornerstone of our global biodiversity preservation strategy as evidenced by the rapidly expanding portfolio of PA lands (Naughton-Treves et al., 2005). Following the establishment of PAs, managers still face numerous challenges to preserving ecological condition and biodiversity (Gaston et al., 2008). Principle among these challenges is that PAs represent only subsets of larger socio-ecological systems (GAO, 1994; Hansen et al., 2011; Nagendra et al., 2010). Processes, organisms, material and energy routinely pass back and forth across PA boundaries that were often drawn for reasons other than biodiversity conservation (Pressey, 1994). Human activity can interrupt ecological flows between PAs and adjacent areas (Hansen and Defries, 2007). Therefore, changes in patterns of human activity in areas surrounding PAs is a topic of concern for PA managers.

Habitat destruction and fragmentation are the leading causes of species loss globally, and many PAs are experiencing declines in biodiversity as a result of human activity on surrounding lands (Newmark, 1985; Parks and Harcourt, 2002; Sanchez-Azofeifa et al., 2003). A number of recent studies have documented rates of land use change around U.S. National Parks (''parks'') that exceed national or regional averages (Davis and Hansen, 2011; Radeloff et al., 2010; Wade and Theobald, 2009). These trends highlight the need to better understand the ecological impacts of land use change around parks.

To address these concerns, the U.S. National Park Service (NPS) established a program to evaluate the ecological condition and monitor trends in condition, of U.S. parks and surrounding areas. The NPS Inventory and Monitoring Program (I&M) (Fancy et al., 2009) has organized over 270 U.S. parks into 32 ecoregional networks where routine monitoring is performed. In the early stages of program development, over 1000 scientists and park-managers from across the country identified and prioritized indicators of ecological condition to monitor (Gross et al., 2011). From this process, landscape dynamics were identified as a high priority indicator (Svancara et al., 2009). Landscape dynamics refers to change in natural land cover types and human land use.

A key challenge for the NPS I&M Program is how to quantify landscape dynamics in ways that are relevant to expected impacts on park biodiversity. A natural first step is to quantify change from past to present. Ideally, species-specific data and spatially-explicit population demographic models would be used to interpret how land use and cover change has influenced key-species since the time of European settlement and/or park establishment. However, such ideal datasets and models are not presently available. A long recognized alternative to the species-specific (termed fine-filter)

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approach is a coarse-filter approach where habitat types rather than species are the units of analysis (Hunter et al., 1988). Many organisms and ecological processes are associated with particular habitat types. Thus, quantifying change in habitat, which is easier to measure, is informative about change in species, which is more difficult to measure.

Present-day conservation in U.S. parks is constrained by landscape context and land use history. Some parks were little impacted by human-settlement at the time of their establishment, are large in size and mostly surrounded by other publicly-managed lands. For these parks, contemporary challenges lie predominantly in managing existing and future land use change so-as to minimize impacts to park condition. Other parks were established following intensive human use, are small in size and exist within a matrix of private lands. For these parks, challenges are focused on preserving what is left of key habitats, restoration and maintaining connectivity to regional PA networks.

The present study outlines methods to establish benchmark measures of land use change against which to compare future observations and prioritize conservation efforts. To demonstrate the utility of these methods we apply them to four case study-areas. We drew on the biophysical setting (bps) data layer of the LANDFIRE program (Barrett et al., 2010; USFS, 2010) to represent habitat types of interest. This dataset was developed as a science-based, nationally consistent layer of ecosystem reference conditions based on simulated historical ranges of natural variation (Keane et al., 2002, 2009). We overlaid areas of present-day human land use on modeled historical habitat to estimate the extent of fragmentation to the present-day. The objectives of the study were to:

1. Quantify change in the aerial extent and spatial pattern of key habitats in and around parks due to human land use intensification.
2. Use the results to identify the habitats that have been most fragmented and therefore are highest priorities for further research, management and conservation action.

2. Material and methods

2.1. Study-areas

The study focuses on four study-areas containing seven parks and surrounding lands (Fig. 1) including: Delaware Water Gap National Recreation Area and Upper Delaware River Scenic and Recreational River (hereafter referred to together as "Delaware Water Gap"); Rocky Mountain National Park (Rocky Mountain); Yellowstone and Grand Teton National Parks along with the John D. Rockefeller Jr. Memorial Parkway (Yellowstone); and Yosemite and Sequoia-Kings Canyon National Parks (Yosemite). Parks were selected as part of a larger study based on availability of data and familiarity with the sites (see Gross et al., 2011 for a complete description of the larger study).

Determining the area of analysis, or protected-area-centered-ecosystems (PACEs), was done following the methods of Hansen et al. (2011) (see Appendix 1 of Hansen et al., 2011 for methods details). These methods identify areas surrounding parks where land use change is most likely to affect park condition. All analyses that follow were performed across the entire PACE area including within park boundaries. A short summary of each PACE, including recent trends in land use and expected results is provided below.

2.1.1. Yellowstone

Yellowstone parks were established in the late 18- and early 1900s to protect wildlife habitat. They are largely surrounded by other public lands (mainly U.S. Forest Service, USFS) and have experienced little land use change in their surroundings since the time of their establishment (Davis and Hansen, 2011). The Yellowstone PACE is over 32,000 square kilometers in size and spans portions of Montana, Wyoming and Idaho (Fig. 1). Sixteen-percent of the PACE outside of parks is privately-owned and is rural to undeveloped in character. Large farms and ranches that are hundreds to over one-thousand hectares in size are typical of this region. Private-lands tend to be in lower-elevation river-valleys covered by grassland (mix of species) and sagebrush (*Artemisia* spp.), as well as riparian areas of diverse vegetation including deciduous-trees (*Populus* spp.) and shrubs (*Salix* spp.). Higher-elevation public lands are mostly forested with a mix of conifer species (*Pseudotsuga*, *Abies* and *Pinus* spp.). It was expected that the Yellowstone study-area has been little impacted by land use change relative to other study-areas (Davis and Hansen, 2011).

2.1.2. Yosemite

Yosemite parks were established in the late 1800s to mid-1900s to preserve their scenic and recreational value. The parks are largely surrounded by public lands (USFS) and have experienced little land use change since the times of their establishment (Davis and Hansen, 2011). The Yosemite PACE is over 38,000 square kilometers in size and spans mountainous portions of eastern California (Fig. 1). Twenty-eight percent of the PACE is on private-land that is undeveloped to exurban in character. Private-lands tend to be lower-elevation forest and woodlands of mixed-conifer (*Pinus* spp.) and deciduous (*Quercus* spp.) species transitioning to higher-elevation public lands of conifer (*Pinus* spp.) forests and open meadows (mix of alpine and subalpine species). It was expected that the Yosemite study-area has been little impacted by land use change relative to other study-areas (Davis and Hansen, 2011).

2.1.3. Rocky Mountain PACE

Rocky Mountain National Park was established in 1915 to protect high-elevation areas along the Colorado continental-divide for its scenic and recreational value. It is surrounded by public (mostly USFS) land and has experienced moderate land use change since the time of its establishment (Davis and Hansen, 2011). The Rocky Mountain PACE is almost 10,000 square-kilometers in size and is contained entirely within the State of Colorado (Fig. 1). Twenty-seven percent of the PACE area is on private-lands that are rural to suburban in character. Private-lands tend to be moderate-elevation mixed conifer- (*Pinus* and *Pseudotsuga* spp.) and deciduous (*Populus* spp.) forest that transition to higher-elevation public lands of subalpine conifer (*Picea* and *Abies* spp.) forest and substantial areas of lightly-vegetated (krummholz) rocky ground at the highest-elevations. It was expected that the Rocky Mountain study-area has been moderately impacted by land use change relative to other study-areas (Davis and Hansen, 2011).

2.1.4. Delaware Water Gap PACE

Delaware Water Gap parks were created in the mid- to late-1900s following sometimes intense human land uses. The parks were established to protect water-quality and recreational opportunities of the Delaware River. Surrounding lands are mostly in private ownership and have undergone rapid land use change over the last several decades (Davis and Hansen, 2011). The Delaware Water Gap PACE is over 14,000 square kilometers in size spanning the Pennsylvania and New York state borders (Fig. 1). Eighty-one percent of the Delaware Water Gap study-area is on private lands that tend to be suburban to exurban in character with numerous small towns distributed throughout. What little publically-owned land does exist is managed as state-forest. The parks are centered on low-elevation riparian areas that transition up often steep rhododendron (*Rhododendrun* spp.) ravines to higher-elevation eastern-deciduous (*Quercus*, *Acer* and *Carya* spp.) and hemlock (*Tsuga*

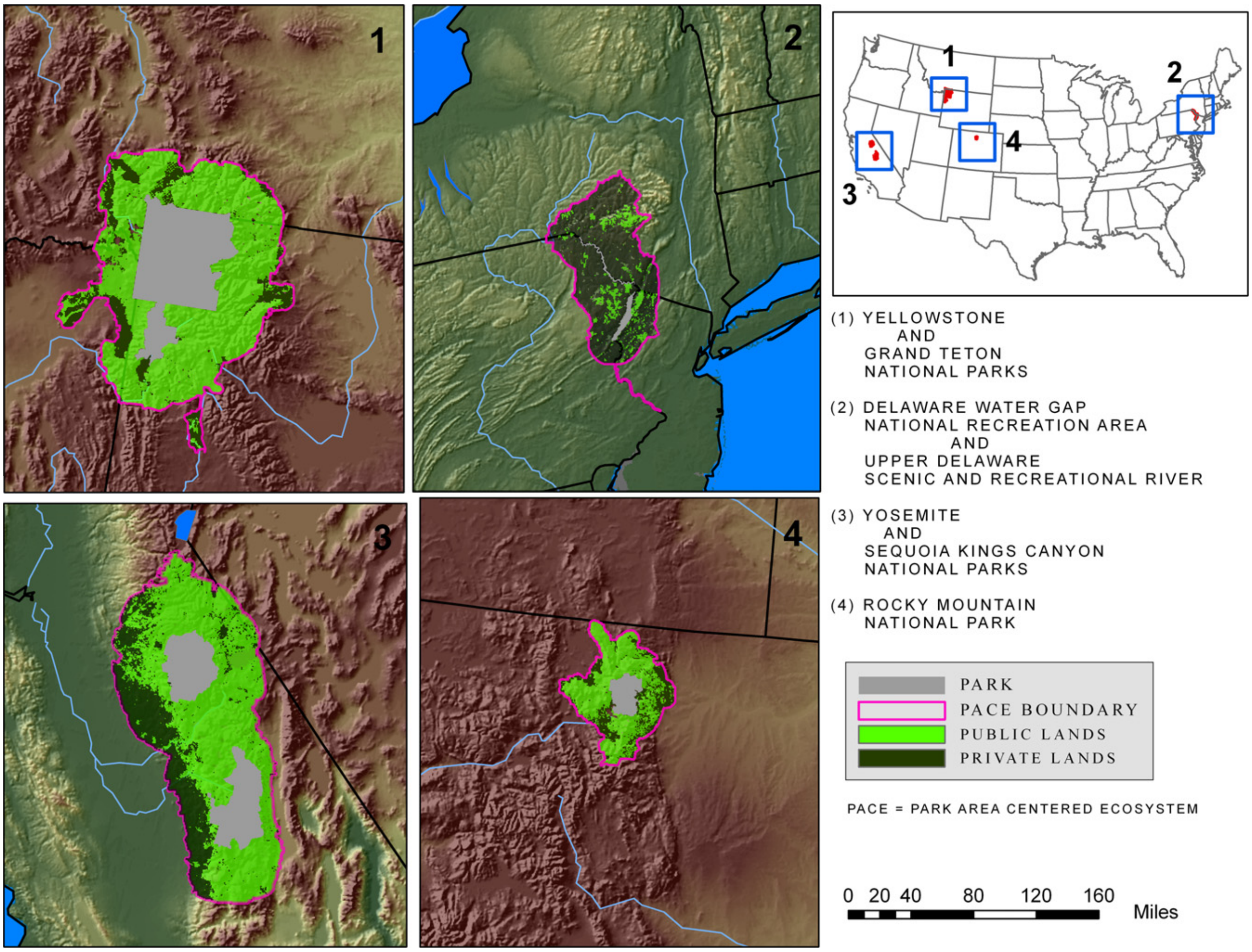

Fig. 1. Study-area. Includes park boundaries, areas of analysis and land ownership.

canadensis) forests. It was expected that the Delaware Water Gap study-area has been highly impacted by land use change relative to other study areas (Davis and Hansen, 2011).

2.2. Generating historical reference conditions

The collaborative multi-agency LANDFIRE program (Barrett et al., 2010; USFS, 2010) has published a suite of nationally consistent, scientifically-based data layers for use in land management and research activities. The LANDFIRE biophysical setting (bps) layer was developed based on the relationship between current vegetation communities (International Terrestrial Ecological Systems or ITES) (Comer et al., 2003) and their biophysical settings; as well as transition probabilities associated with different types of disturbance events, and simulated historical ranges of variation in disturbance return intervals and intensities (FRCC, 2010; Keane et al., 2002). It was created as a layer of reference conditions to assess departure by present-day vegetation communities from historical conditions. The bps layer can be interpreted as the "central-tendency" of vegetation communities at distinct locations on the landscape under a static climate envelope in the several-hundred years preceding European settlement, (for a complete description of methods see Barrett et al., 2010; FRCC, 2010). We generalized the historical land cover types mapped by LANDFIRE bps to 26 coarse-scale habitats thought to be important to species preservation. We chose this approach in contrast to empirical observations of recent historical conditions or other layers of potential vegetation, for the following reasons:

i. To provide a benchmark reference of change (from presumed no human activity to the present-day) against which to compare recent and future change. The present effort is seen as complimentary to other studies that document recent land use and cover change around a few parks over the last 50 years (see Narumalani et al., 2004 and Wang et al., 2009 for two examples).
ii. The LANDFIRE bps layer models different successional stages of potential vegetation communities under assumed natural disturbance regimes. It therefore makes an important improvement on other layers that typically model vegetation communities as only being in their "climax" state. The present methods should capture land use impacts to disturbance-maintained early-successional habitat that rarely, if ever, achieves a climax state. They should also estimate loss of early-successional habitat as a result of land-use-change-mediated impacts on disturbance regimes (Gallant et al., 2003).

We worked with park-managers to identify the six to eight key habitat types in and around their parks. Habitat types were chosen based on their present prevalence on the landscape and importance to supporting wildlife and other biodiversity. We also created a habitat type that captured all *Other natural vegetation*. Habitat layers were spatially clipped to each PACE area for use in further analysis.

2.3. Identifying developed-areas

The present study identified human-dominated, intensively-managed, or areas under permanent human infrastructure as being developed for human use. This included primary and secondary roads, areas under active agricultural management, commercial and industrial areas and areas where residential housing densities were above one home per 80 acres. This housing density threshold was chosen following the work of others who identify one home per 80 acres or less as low-density rural residential or undeveloped (Brown et al., 2005; Theobald, 2005). The goal was to choose a threshold housing density that conservatively identified areas that have been impacted by human land use; although the ecological impacts of low-density residential development remains an active area of research (Turner, 2005). Data layers describing human land use (Table 1) were spatially combined into a single layer using ArcGIS 9.2 (ESRI, 2006). Resulting maps represent conditions for the time-period 2000–2009. The only pre-processing of these data was the addition of a buffer to the roads layer. Roads were buffered with an approximation of actual road-footprint width based on road class.

2.4. Overlay analysis

Developed-areas were overlaid on and used to erode historical habitats to create present-day conditions. In present-day conditions it is assumed that habitats that have become developed for human use are functionally lost to the ecosystem. Ownership boundaries were determined using a modified version of the Conservation Biology Institute's Protected Area Database (version 4.6), produced by Theobald and Mahal (unpublished results, 2009).

2.5. Habitat composition and pattern analysis

Habitat change was quantified in a before and after framework where percent remaining (for area metrics) or percent change (for pattern metrics) were the measures of interest. Total change and proportions of change on public versus private land was also quantified. Finally, the range of total habitat remaining on private lands across habitats (highest percentage remaining minus lowest percentage remaining) indicated the degree to which some habitats had been disproportionately affected by human-activity at the reprieve of others. To clarify, a random spatial arrangement of both habitat classes and human land use would likely result in an even distribution of loss across habitats. Spatial-clustering of both human land use and habitat classes on private lands would result in large losses of some habitats and small losses for others. Landscape pattern-metrics included two simple, complementary measures and their variation: mean patch area; coefficient of variation in mean patch area; Euclidean distance to nearest neighbor (ENN) of the same patch class; and coefficient of variation of ENN. Change in landscape pattern metrics indicate the degree to which the spatial pattern of habitat patches has changed from past to present. Change in mean patch size describes how total habitat area is being lost (i.e. a little from each patch or total loss of some patches). This is significant because smaller patches often support smaller local populations that may be more susceptible to extinction events (Leitao et al., 2006). A change in the distance to the next patch of the same habitat type (ENN) describes where habitat is being lost. An increase in ENN distance can indicate isolation of populations from neighbors, leading to a less robust population overall (Leitao et al., 2006). Loss of area and change in pattern together describe the effects of fragmentation. Analyses were performed using FragStats 3.3 software (McGarigal et al., 2002).

3. Results

3.1. Summary for all parks

The vast majority of habitat area remains in Yellowstone and Yosemite (92% and 89% on average), most remains in Rocky Mountain (78%) and some remains at Delaware Water Gap (34%) (Figs. 2–5 and Supplementary material Table 1). No habitat type in the study had more than 80% of its area remaining on private lands or less than 82% remaining on public lands. Change in habitat pattern largely mirrored changes in area with a few exceptions that are mentioned in study-area highlights below (see also Fig. 6 and Supplementary material Table 2). The summary of results that follows discusses only the most notable (either largest or expected to be most impactful) habitat changes by study-area. In summary, the methods of the present study captured trends in land use change, impacts to specific habitat types and differences in impacts by study-area.

3.2. Summary of results by study-area

No habitat type in the Yellowstone PACE had less than 80% of its total area remaining and all habitats were largely undisturbed by human activity on public lands (Figs. 2 and 6 and Supplementary material Table 1). There was modest variation (26%) in this result on private lands meaning that some habitats experienced greater change than others. Habitats with the least area remaining included those that are underrepresented on public lands such as *Sagebrush*, *Riparian* and *Deciduous.* The *Whitebark pine* habitat had the most reference area remaining. Change in landscape pattern metrics mirrored habitat area results with *Sagebrush* experiencing the largest change in mean patch size while *Grassland* and *Douglas-fir* displayed moderate decreases in mean patch size (Supplementary material Table 2). On average, Yellowstone habitats had 68% of their reference area remaining on private lands, 98% on public lands and 92% overall.

No habitat type in the Yosemite PACE had less than 75% of its reference area remaining, meaning that most of this PACE remains largely undisturbed by human activity (Figs. 3 and 6 and Supplementary material Table 1). However, some habitats located to the west of the parks have experienced moderate intensities of land use change as evidenced by a range of 34% of area remaining

Table 1
Data sources and resolution for mapping land use.

Developed area	Data source	Spatial resolution
Transportation corridors (primary, secondary and private roads, railroads)	TIGER lines file; U.S. Census Bureau	Approximation of actual footprint
Agricultural	National Land Cover Dataset 2001	30 m
Commercial and industrial	National housing density database from SERGoM[a] model (Theobald, 2005)	30 m
Residential housing	National housing density database from SERGoM[a] model (Theobald, 2005)	30 m

[a] SERGoM = Spatially Explicit Regional Growth Model.

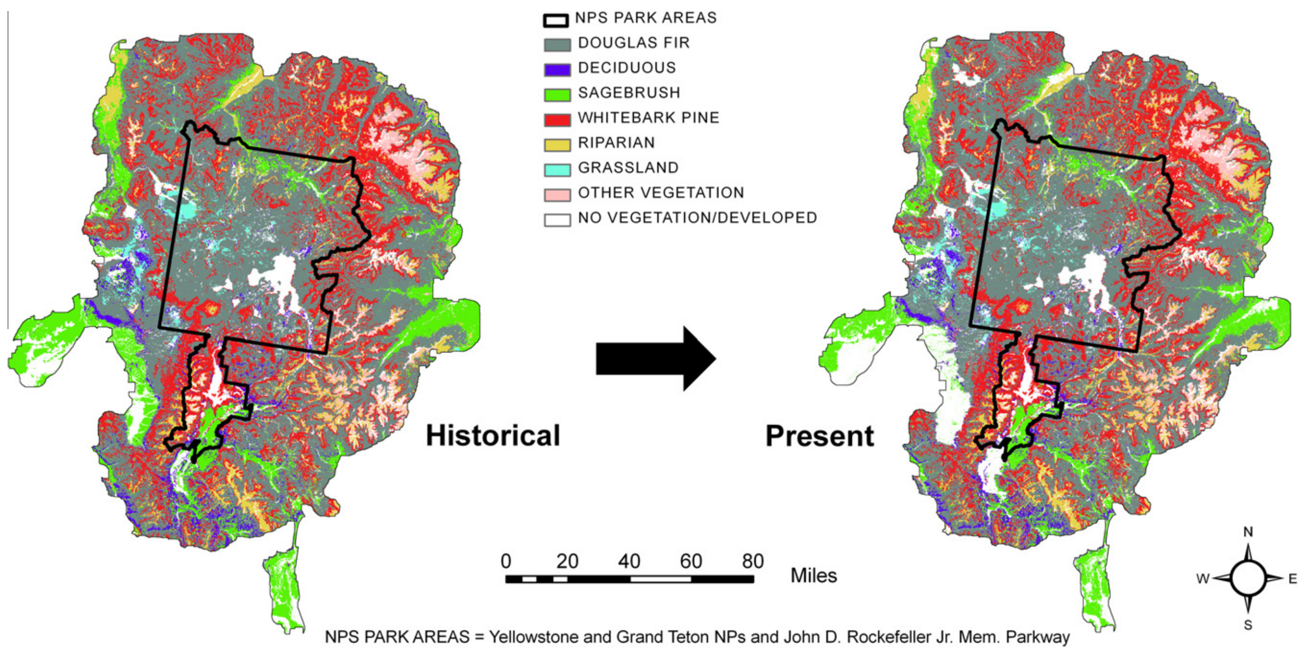

Fig. 2. Historical versus present-day habitat for the Yellowstone study-area. Yellowstone has been minimally impacted by land use to date.

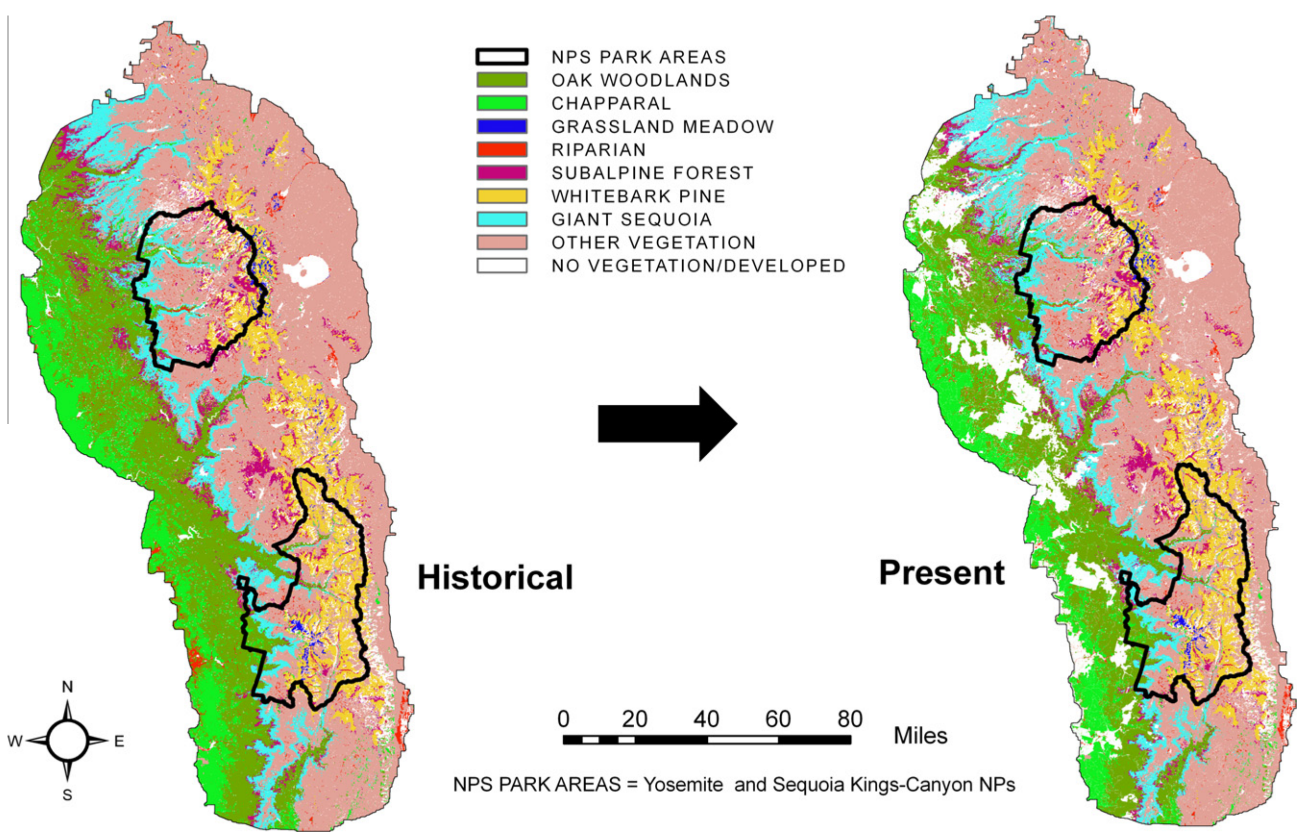

Fig. 3. Historical versus present-day habitats for the Yosemite study-area. Some areas to the west of Yosemite parks have been impacted by land use.

on private lands. The *Oak forest and woodlands*, *Riparian* and *Chaparral* habitats had the least reference area remaining while *Grassland meadow* and *Whitebark pine* habitats had the most. Change in landscape pattern metrics largely mirrored change in habitat area with one exception that *Giant Sequoia* experienced a 65% decline in mean patch size. On average, 63% of habitat remained on private lands, 98% on public lands and 89% overall.

Two habitat types in the Rocky Mountain PACE had less than 70% of total reference area remaining while two others had more than 90% of total remaining. This translated to a large range (51%) in area remaining on private lands. Areas of intense human activity fell between the park and Interstate 70 corridor, around the community of Estes Park, CO and in the eastern foothills near Denver, CO. The *Grassland meadow* habitat had only 65% of its total

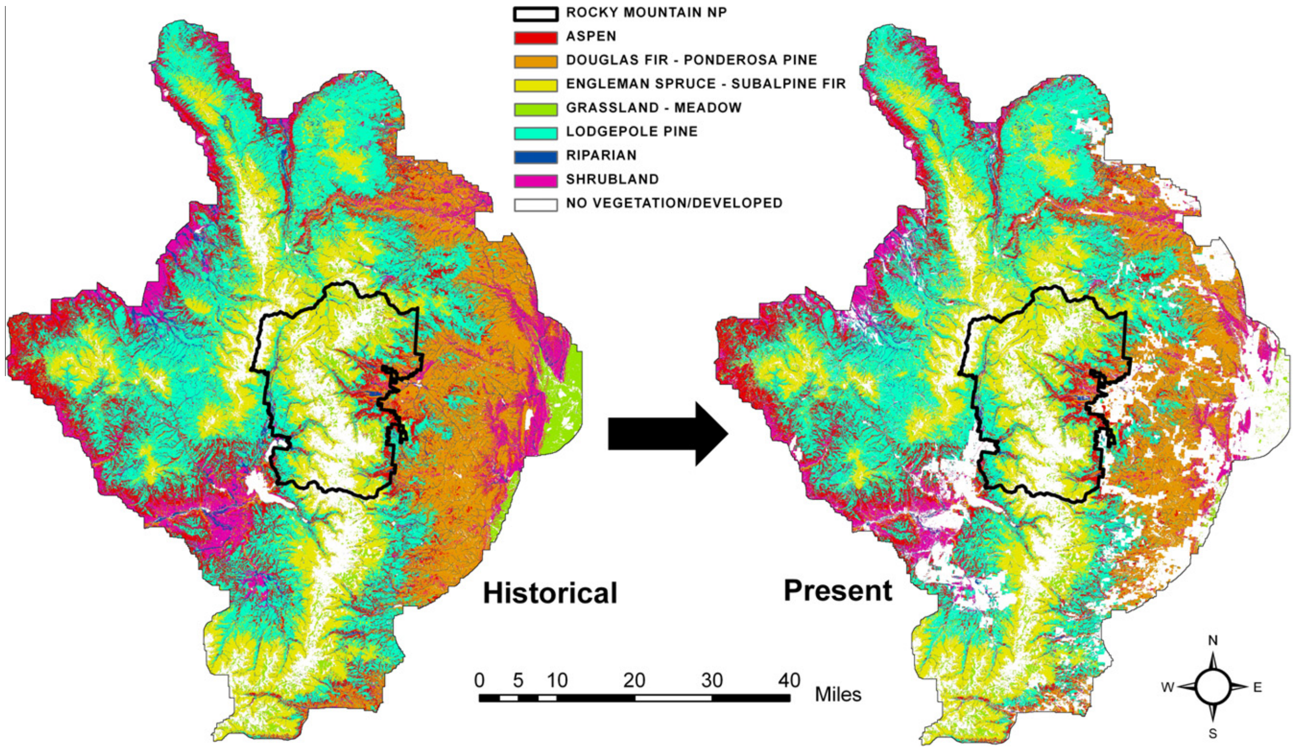

Fig. 4. Historical versus present-day habitats for the Rocky Mountain study-area. Some areas to the south (towards the I-70 corridor) and east (towards the Denver metropolitan area and areas around Estes Park, CO) have been impacted by land use.

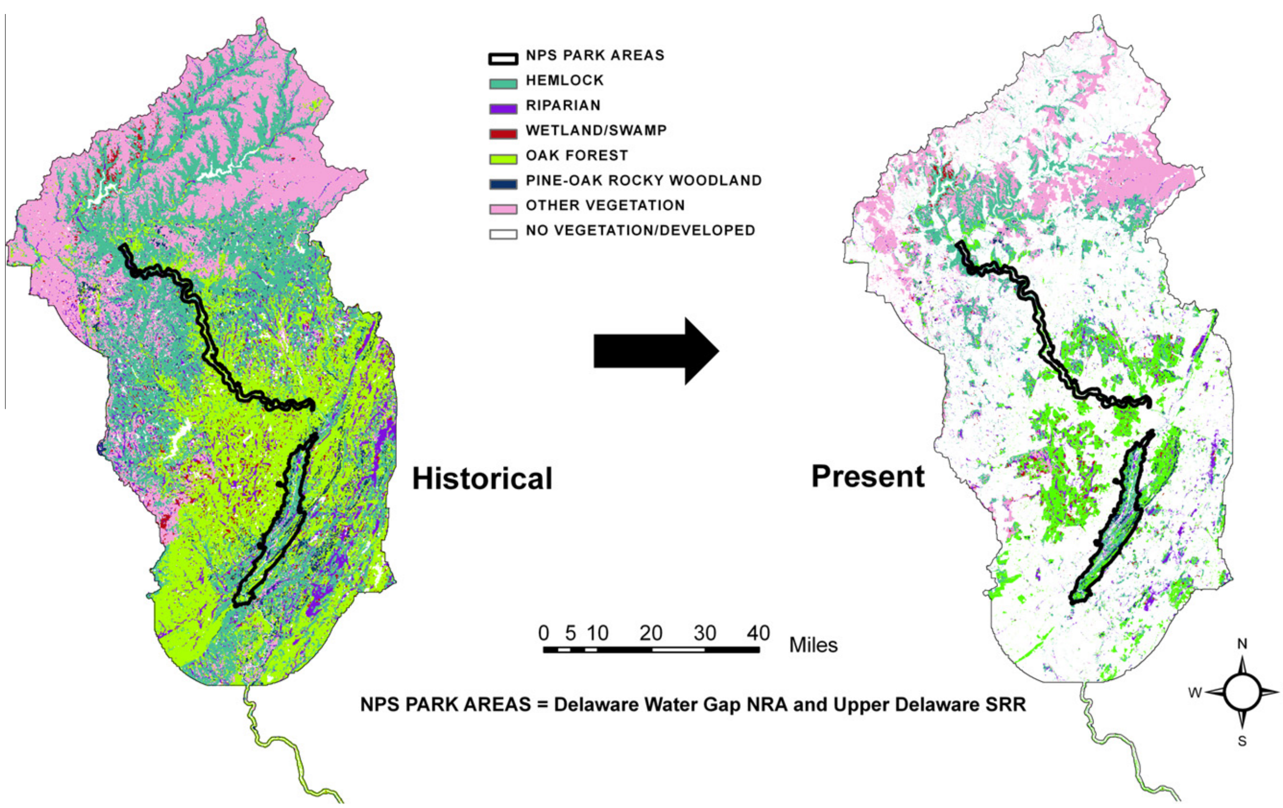

Fig. 5. Historical versus present-day habitats for the Delaware Water Gap study-area. Land use impacts on habitats have been uniform and heavy, although these may be overestimates based on a threshold housing density that is inappropriate for many eastern landscapes.

reference area remaining (14% remaining on private land), and the *Shrubland* ecosystem type had 70% remaining (54% remaining on private land). This is in contrast to *Engelmann-spruce-subalpine fir* that had 100% of its habitat area remaining and *Lodgepole pine* that had 91% remaining. Change in landscape pattern metrics largely mirror change in habitat area with *Grassland meadow*, *Riparian*

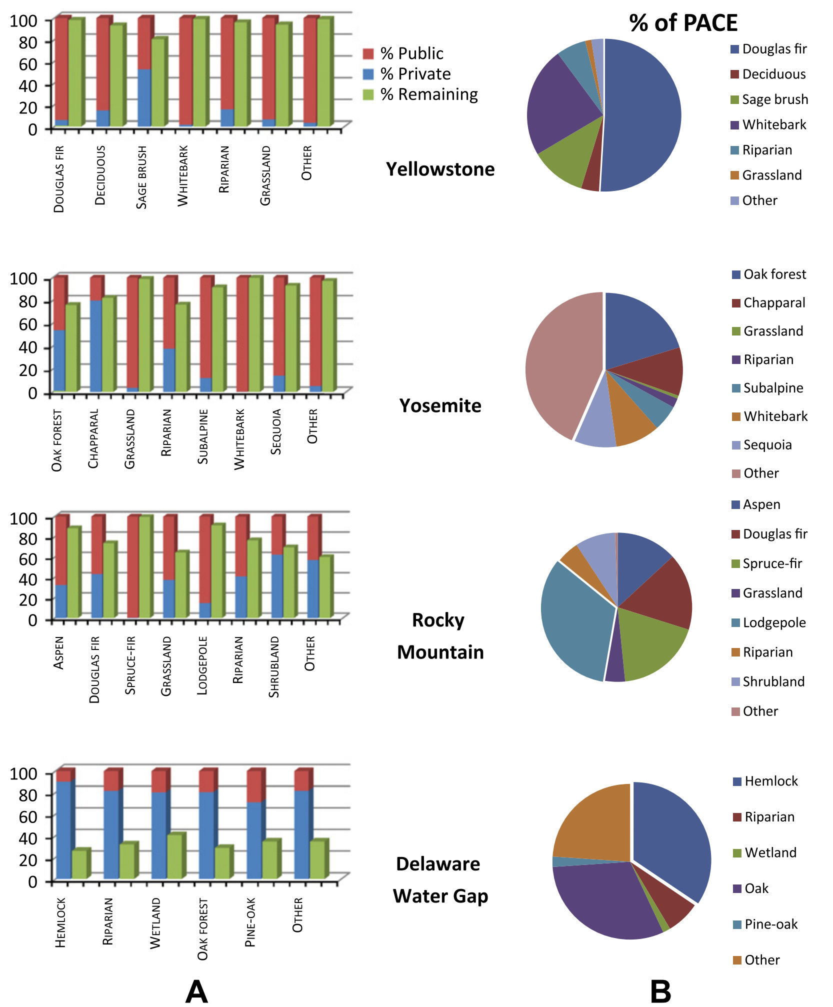

Fig. 6. (A) Change in habitat area from pre-European settlement to the present-day. (B) Percentage make-up of habitats within study-areas.

and *Shrubland* all experiencing double-digit percentage declines in mean patch size and modest increases in the distance to the next patch of the same habitat type. On average, Rocky Mountain PACE habitats had 47% of their area remaining on private lands, 97% on public lands and 78% overall.

No habitat type in the Delaware Water Gap PACE had more than 30% of its reference area remaining and there was the least variation in the study (16%) of area remaining on private lands. *Hemlock* had the least area remaining (26%) while both *Oak forest* and *Riparian* each had around 30% of their reference area remaining. *Pine–oak rocky woodlands* had only 12% of its reference area remaining on private lands. On public lands, all habitat types had at least 80% of their reference area remaining and most had over 90%. Landscape pattern metrics largely mirrored area change results with *Hemlock* mean patch size decreasing by 94% and both *Oak forest* and *Other vegetation* decreasing by at least 90%. On average, habitats had 20% of their reference area remaining on private lands, 90% on public lands and 34% overall.

4. Discussion

4.1. Overview of the discussion section

In general, habitats on public lands have been well-protected from human development. However, some habitats are underrepresented on public lands and have lost a significant proportion of their area to land use change on private lands. The following discussion highlights the utility of the present methods, some limitations of the present methods and addresses the conservation implications of results by different patterns of land use change.

4.2. Identifying critical needs for habitat conservation

Habitat loss beyond (often unknown) thresholds is thought to lead to local species extinctions (Rosenzweig, 1995). As such, park-managers and others working for species preservation have a need to identify habitat types that are nearing thresholds that will result in localized species extinctions. The present methods estimate habitat loss from pre-European settlement to the present-day as a result of land use intensification. Other studies have quantified expected species loss given different levels of habitat loss (see Brooks et al., 1999 for an interesting example). Many studies use species-area relationships and predict substantial extinctions when levels of habitat loss exceed approximately 70–80% (although these predictions have been recently been called into question as overestimates; He and Hubbell, 2011). Confusing species-area relationships are time-lags (i.e. extinction debts), sampling issues and the often non-random spatial arrangement of both habitats and human land uses (Seabloom et al., 2002). In the present study, it would seem that most habitats have been sufficiently well-protected to preserve most species as predicted by species-area relationships. However, some habitats are quickly approaching or have already exceeded levels of habitat loss that could lead to a large number of species extinctions should human land use continue to intensify or extinction debts catch up to habitat degradation that has already occurred. These habitats deserve special attention and their protection may be critical to achieving park preservation goals. The present study demonstrates methods to help prioritize habitat conservation needs in the face of land use change.

4.3. Scope and limitations

A consideration in applying the results of the present study is related to unknown affects of future climate change on vegetation communities. The LANDFIRE bps layer was developed based on a current climate envelope which may not be representative of future climates. Climate change has the potential to alter the relationship between habitat types and their current position on the landscape. However, we expect that the results of the present study remain relevant in the face of future climate change for several reasons. First, the thematic generalization undertaken by the present study should buffer against small changes in climate except possibly at the very edges of habitat patches where change will likely occur more readily (i.e. ecotones). This is based on prevailing understanding of incremental upslope (Moritz et al., 2008) and poleward (Parmesan and Yohe, 2003) shifts in species distributions under climate warming (although surprises may exist such as is detailed in Crimmins et al. (2011)). Thematic generalization increases in size each habitat patch and this should decrease the proportion of each patch that shifts under incremental upslope (or poleward) patch migration. Second, it is expected that changes in climate will significantly interact with changes in land use to determine future ecological outcomes of global environmental change and therefore mapping areas that have been significantly altered by human activity remains relevant in the context of climate change (Heller and Zavaleta, 2009; Root and Schneider, 2002; Running and Mill, 2009). Finally, a biophysical, central-tendency approach to mapping ecosystem types may be more robust to climate change than maps of present-day (or near-term historical) vegetation communities. This is because present-day communities may represent assemblages of species that occur only rarely in these settings and may therefore be more susceptible to modification by small shifts in climate or associated shifts in disturbance regimes. This idea is similar to what Anderson and Ferree (2010) call "preserving the stage" where the authors focus on the geophysical underpinnings of species-diversity as an approach to reserve design under climate change. As attention shifts towards conserving areas adjacent to parks, those involved in planning will need to consider the potential of places to support habitat under different climate change scenarios. This is in contrast to a "business as usual" strategy that considers only what habitat exists on the landscape at present.

The present study focused only on the ecological effects of land use change and not on other possible modes of habitat degradation that may be important in these study-areas; this decision effects the interpretation of our results. For example, *Whitebark pine* in both Yellowstone and Yosemite is an important habitat type, but was not found by the current study to require special conservation attention. However, *Whitebark pine* habitat throughout both study-areas is seriously threatened by white pine blister rust (*Cronartium ribicola*) and mountain pine beetle (*Dendroctonus ponderosae*) and as a result does in fact merit special conservation attention (Bockino and Tinker, 2012; Maloney, 2011). *Hemlock* in Delaware Water Gap and the wooly adelgid (*Adelges tsugae*) provide another example of a habitat that is severely threatened by degradation brought about by a change-agent other than land use. We focus on land use because its ecological effects on parks are understudied (Hansen and DeFries, 2007) and unlike other drivers of change, there are ample opportunities to ameliorate adverse effects. The results of the present study should be evaluated within a larger body of knowledge concerning major drivers of ecological change in study-area ecosystems.

A fundamental assumption made the authors of the current study is that a generalization of the LANDFIRE bps layer does an adequate job of representing historical landscape condition. In unpublished work, the results of extensive efforts to validate this data layer using present-day maps of vegetation communities of known accuracy were inconclusive (Piekielek, 2010, unpublished). This finding is likely a result of differences in contemporary patterns of large-scale disturbance (especially those that cross park boundaries) versus patterns of disturbance as modeled by the LANDFIRE program. The central-tendency approach used by LANDFIRE to model habitat (as modified by disturbance) should not be expected to perfectly match real conditions at any given point in time including the present-day. What a central-tendency approach does do (and which is not captured by alternative methods) is offer reasonable estimates of early-successional habitat that has been lost to land use change either directly (as represented by the current study) or indirectly through human modification of disturbance regimes. As has been noted by others, there does not presently exist satisfactory ways to validate modeled historical conditions (Keane et al., 2009). However, it is the opinion of the authors that the LANDFIRE bps layer is the best data layer presently available to represent historical landscape conditions of coarse-scale habitats in and around U.S. parks.

Habitat patches in the present study were treated as being functionally lost to the ecosystem following human development. For agricultural and urban land uses that replace the majority of native land cover this is likely a safe assumption. For other land uses, such as low-density residential development this assumption is tenuous and deserves further consideration and study (Turner, 2005). To address uncertainty, we used a conservative threshold of one home per 80 acres. This threshold is likely appropriate for the most human-intolerant species (usually apex predators), but may be less appropriate for human-tolerant species. There is little published research on a threshold housing density beyond which species no longer use habitat patches. Regardless of the threshold chosen, the relative pattern of change (habitats within PACEs compared to each other) will remain the same and is the primary focus of the present study.

A final assumption required of the present methods is that roads of a certain size will fragment habitat patches even within parks. In the present analysis, roads were found to be primarily responsible for area and especially pattern change within parks. Many park roads have lower speed limits and traffic volumes than neighboring state and federal roads. Consequently, they may not be a barrier for large mobile species. However, for smaller less mobile species, even park roads may be a barrier to movement and serve to isolate and threaten local populations. The extent to which different types of roads create a barrier to species movement across park landscapes remains an active area of research and one that could contribute to future implementations of the present methods (Benitz-Lopez et al., 2010).

4.4. Conservation and management implications

Each study-area exemplifies a specific set of conservation challenges that are associated with different patterns of land use change. As such, each study-area is also likely representative of other PACEs around the country. Characterizing each set of conservation challenges provides decision-support for managers and contextualizes the issues faced by parks. For PACEs like Yellowstone, the principal conservation challenge is to maintain landscape condition in its present or near-present state. If not managed, land use intensification will likely drive Yellowstone (and similar PACEs) toward a landscape condition more similar to Rocky Mountain. As is common for western parks, many of the most productive habitats (and hence most important for biodiversity conservation; Wright, 1983) are on public lands (Scott et al., 2001; Gude et al., 2007). Therefore, paying particular attention to habitats that are underrepresented on public lands and have been the subject of land use change represents a conservation challenge with which the present methods may help. For Yellowstone specifically, *Sagebrush* provides an instructive example. What *Sagebrush* habitat is left supports a number of wildlife species that are already of special management concern (pronghorn, *Antilocapra americana* and sagegrouse, *Centrocerous urophasianus* for example). Management action within park boundaries to protect these habitats could include: avoiding areas for future development of visitor services and park operations; and closing or limiting visitor use in these areas during critical times of year for species of concern. Restoration projects could also be undertaken where they are feasible. The central-tendency based approach taken by the present study may be especially useful for identifying candidate areas for restoration in that maps highlight areas where present-day habitat deviates from its typical biophysical setting (although climate change may modify biophysical settings in the future). Outside of parks on private lands, easements and other community conservation tools often employed by non-governmental organizations (NGOs) can be used to protect habitat from future development. Swenson and Franklin (2000) and Gude et al. (2006) both provide nice examples of modeling expected future development near parks in order to identify areas for targeted conservation projects. In these examples, the present methods could be used to identify the highest priority habitat types for conservation and simulations of future development used to identify specific property parcels to target for protection. Results produced by the present study may be especially useful to parks and NGOs alike to identify collaborative conservation opportunities on private lands surrounding parks.

The Yosemite and Rocky Mountain PACEs appear to be on similar trajectories of development. This trajectory is defined by PACEs comprised of a high proportion of public lands, but with expanding exurban communities in their surroundings. Results for both parks suggest that only certain habitat types are at risk while others remain insulated from change by ownership or accessibility. In the case of Rocky Mountain, front-range Colorado foothills that are adjacent to public lands are being developed for residential uses due to the natural amenities that they provide (Leinwand et al., 2010). A similar amenity-based population migration is underway in the Sierra foothills as is detailed by Walker (2003) and Oeffler and Steinicke (2006). This is representative of a national trend that has been noted by others (Brown et al., 2005). Two potential benefits of this pattern of change are that: (1) spatially-clustered development limits the number of entities (local governments for example) with whom planners have to work in order to manage change; and (2) new residents often relocate because they value natural amenities and therefore may be more supportive of local conservation efforts (although this is by no means a guarantee). Regarding this last point, the stewardship behavior and environmental consequences of new rural landowners is nicely developed by Gill et al. (2010) who draw heavily on social research performed in the Greater Yellowstone Ecosystem (Gosnell and Travis, 2005; Gosnell et al., 2006, 2007; Haggerty and Travis, 2006).

The Delaware Water Gap is representative of many parks in the eastern US that were established following human settlement and have recently undergone rapid suburban and exurban expansion in their surroundings. If the assumed one home per 80 acre threshold used in the present study is close to accurate for these ecosystems, then they are severely at risk. If this is the case, then the preservation of what habitat outside of parks remains, as well as maintaining connectivity to a regional network of public lands, are likely the top conservation priorities (Goetz et al., 2009). However, these parks were founded following decades of sometimes intense human uses including agriculture, logging, and even warfare (Wright, 1999). Native species that were especially sensitive to human activity (the eastern cougar, *Puma concolor couguar* for example) and for which the one home per 80 acre threshold probably best applies, were lost from these ecosystems long before parks were establishment. Therefore, further species loss based on current expansion of low-density residential development seems unlikely. Delaware Water Gap provides an example of a complex landscape restoration project whose successful completion is threatened by land use intensification in its surroundings. Understanding what biophysical setting means to a PACE that has already been fundamentally altered by human activity provides a major challenge to the application of the present results in many eastern landscapes. At the very least, results of the present study may focus conservation attention on the few most critically threatened habitats that might otherwise be missed in the face of what appears to be a uniform "sea" of change.

4.5. Conclusions

The present study demonstrates the importance of understanding and monitoring landscape dynamics around U.S. parks. Each PACE in the current study is experiencing human activity in their perifory that is representative of broad-scale patterns of land use change across the country. As such, park-managers and others working for environmental conservation can learn from the challenges faced and solutions developed by others who are operating within similar constraints.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2012.05.003.

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