



Decline of forest interior conditions in the conterminous United States

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Forest fragmentation threatens the sustainability of forest interior environments, thereby endangering subordinate ecological attributes and functions. We analyzed the spatial patterns of forest loss and gain for the conterminous United States from 2001 to 2006 to determine whether forest interior environments were maintained at five spatial scales. A 1.1% net loss of total forest area translated to net losses of 3.2% to 10.5% of forest interior area over spatial scales of 4.41 ha to 5,310 ha. At the 65.6-ha scale, the reduction of forest interior area was 50,000 km² – almost double the net loss of total forest area. The pervasive discrepancy between total forest loss and forest interior loss indicates a widespread shift of the extant forest to more fragmented conditions, even in regions exhibiting small net changes in extant forest area. In the conterminous United States, trends in total forest area underestimate threats to forest from forest fragmentation.

Sustaining many of the ecological values of forests requires maintenance of forest interior environments^{1–7}. Most forests are naturally extensive, and as they become fragmented a variety of physical and biological mechanisms begin to limit their capability to support the ecological attributes and functions that depend on interior environments^{6,8–12}. Thus, spatial-temporal trends in forest interior area are often taken as leading indicators of subordinate ecological conditions^{2,4,13,14}. Continental to global forest monitoring tends to focus on the total area and protected status of forest^{15–18}. Such monitoring may not adequately detect trends in forest interior area because “interior” is a contextual attribute that depends on the spatial arrangement of forest area at multiple spatial scales¹⁹. Furthermore, the monitoring of forest interior should account for the spatial patterns of forest loss and gain as they are superimposed upon an initial forest pattern^{20,21}. The objective of this study was to determine whether the spatial patterns of forest change from 2001 to 2006 effectively maintained forest interior area in the conterminous United States.

Forest interior is commonly conceived either in terms of distance to nonforest conditions, or in terms of local dominance of forest conditions. In the first case, forest interior comprises the forest area that is more than a specified distance from nonforest. This approach is typically used to evaluate ecological “edge effects^{6,9,22}.” In the second case, forest interior is the forest area which exists in forest-dominated neighborhoods of a specified size. This approach is more often used as a coarse-filter indicator of ecological attributes and functions that occur within a neighborhood^{23,24}. The two approaches yield comparable estimates of forest interior area when applied over the conterminous United States^{25,26}. In this study, we adopted the second approach and evaluated forest interior based on forest dominance in a neighborhood.

The unavoidable dependence of perceived pattern on measurement scale requires analysis of forest interior at multiple spatial scales. Knowledge of forest interior at a single scale is required to understand the ecological attributes and functions which interact with the forest environment at that scale^{24,27}. A multiple-scale analysis can inform a wider range of ecological questions and identifies the range of spatial scales over which forest interior can be said to exist²⁶. Thus, a multiple-scale analysis is more useful than a single-scale analysis when the goal is to assess forest interior as a generic constraint affecting many ecological attributes and functions. Furthermore, forest interior may exhibit net gains, net losses, or equilibrium depending on the scale at which it is measured²⁸. Our analysis of forest interior was conducted at multiple scales by varying the size of the neighborhood within which forest dominance was evaluated.

We identified and mapped forest interior by using land cover maps for 2001 and 2006 which portray forest in the conterminous United States at a spatial resolution of 0.09 ha/pixel^{29,30}. At each date, each extant forest pixel was described by its forest area density (FAD), defined as the proportion of the pixels in a surrounding fixed-area neighborhood that were forest²³. Each extant forest pixel was then labeled as forest



Table 1 | Scale-dependent change in forest interior area from 2001 to 2006. Forest interior area was measured at five spatial scales defined by neighborhood size and was summarized for the conterminous United States

Neighborhood size (ha)	Forest interior area			
	2001	2006	Change	
	(Thousand km ²)	(Thousand km ²)	(Thousand km ²)	(Percent)
4.41	1,419	1,374	-45	-3.2
15.2	1,151	1,102	-49	-4.3
65.6	867	817	-50	-5.8
590	523	482	-41	-7.8
5,310	277	248	-29	-10.5

interior if the associated FAD $\geq 0.9^{31}$. The measurements were repeated using five neighborhood sizes – 4.41 ha, 15.2 ha, 65.6 ha, 590 ha, and 5,310 ha – that were selected to represent several orders of magnitude of measurement scale. To explain the observed trends in forest interior area, the spatial patterns of forest land cover losses and gains were interpreted with respect to FAD in 2001 and 2006.

Results

The total forest area in 2001 was 2,352,000 km². Forest area losses and gains between 2001 and 2006 were 54,000 km² and 27,000 km², respectively, resulting in a net loss of 27,000 km² which represents 1.1% of total forest area in 2001. In comparison, the net loss of forest interior area was at least 29,000 km² with a maximum loss of 50,000 km² for the 65.6-ha neighborhood size (Table 1). The rate of loss of forest interior area increased monotonically with

neighborhood size and was approximately 3 to 9 times larger than the rate of loss of total forest area.

The disproportionate loss rates are explained by the patterns of original forest area, forest loss area, and forest gain area in relation to FAD in 2001 and 2006 (Fig. 1). Overall forest losses tended to follow the distribution of all forest area in relation to FAD in 2001, but the area lost at high FAD values exceeded the area gained by 2006 at high FAD values. As a result, a smaller percentage of the extant forest area was forest interior in 2006. Regional analyses of 36 ecological provinces showed that these observations were typical of a wide range of initial forest conditions (see Supplementary Information online).

In terms of total forest area, most of the forest-dominated ecological sections in the United States exhibited a net loss while net gains were concentrated in sections where forest is not the dominant land cover (Fig. 2a). In comparison, for the 65.6-ha neighborhood size there was a net loss of forest interior area in 175 of 190 ecological

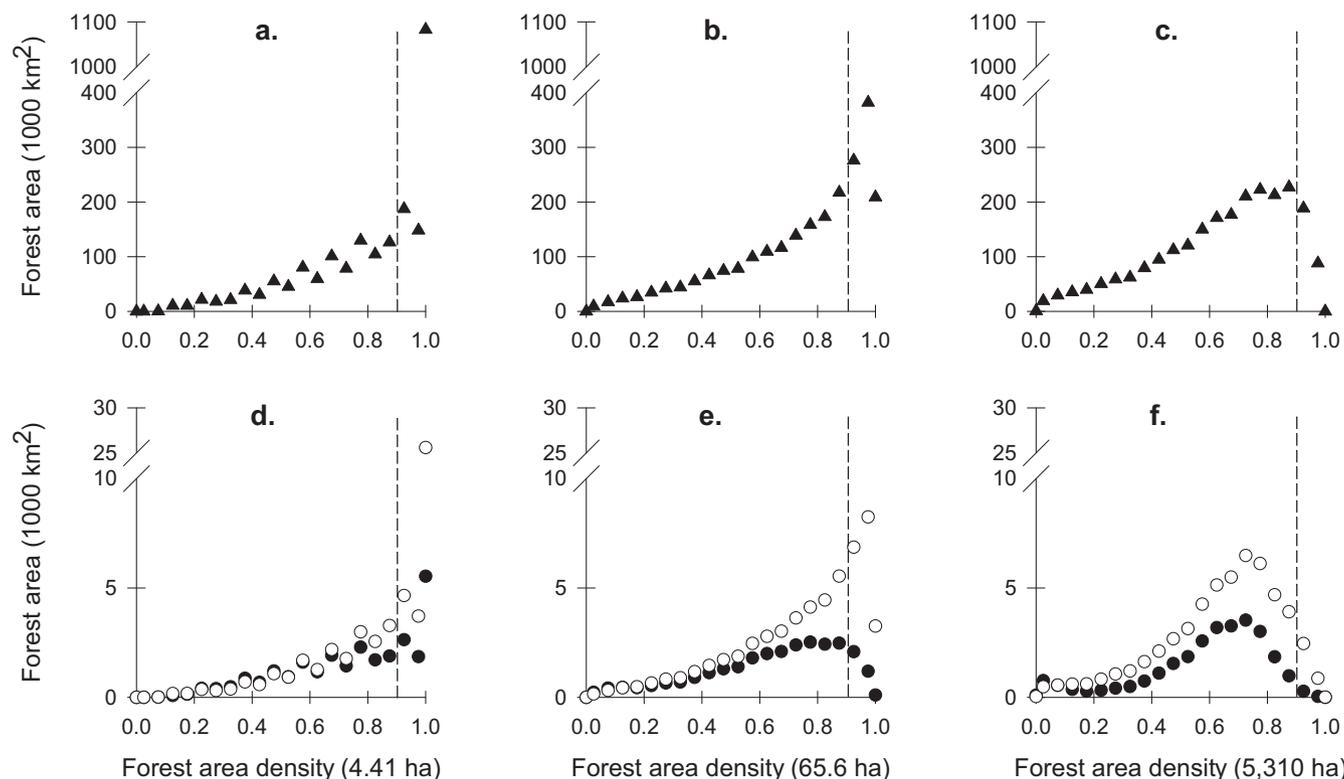


Figure 1 | The area distributions of initial forest, forest gains, and forest losses in relation to forest area density in 2001 or 2006 for three representative neighborhood sizes. Top row: initial forest area in relation to initial forest area density in 2001 (triangles) for neighborhood sizes of (a) 4.41 ha, (b) 65.6 ha, and (c) 5,310 ha. Bottom row: gross forest area lost in relation to initial forest area density in 2001 (open circles) and gross forest area gained in relation to final forest area density in 2006 (closed circles), for neighborhood sizes of (d) 4.41 ha, (e) 65.6 ha, and (f) 5,310 ha. The net change for each value of forest area density is the difference between gross loss and gross gain. Forest interior area for each data series includes the three symbols to the right of the dotted vertical reference lines.

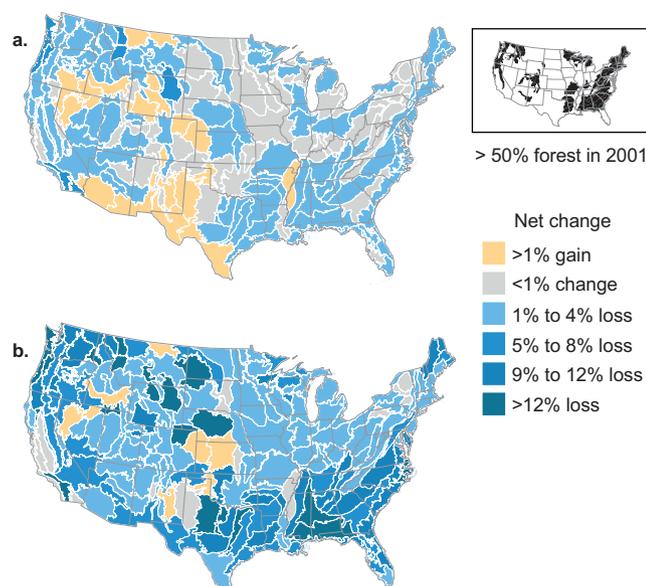


Figure 2 | Net change in forest area from 2001 to 2006. (a) All forest. (b) Forest interior in a 65.6-ha neighborhood. Ecological sections⁴⁴ are shaded and State boundaries are shown for comparison. In the inset map, forest-dominated ecological sections are those that contained more than 50% forest in 2001.

sections, and 74 sections exhibited losses greater than 5% (Fig. 2b). In forest-dominated sections, forest interior area losses greater than 5% were typical in the Pacific Northwest and Southeast regions but were less common elsewhere. The Intermountain and Great Plains regions had relatively low total forest area and the forest interior area changes there had relatively little influence on national statistics. The nearly national extent of differences between total forest loss (Fig. 2a) and forest interior loss (Fig. 2b) suggests a widespread shift in the spatial pattern of the extant forest to a more fragmented condition, including regions exhibiting relatively small net changes in extant forest area.

Discussion

This broad-scale analysis of forest land cover showed that the recent spatial patterns of forest gains and losses have not maintained forest interior area in the conterminous United States. Forest losses tended to follow the distribution of all forest area in relation to FAD in 2001, indicating that preservation of forest interior was not usually an important consideration when forest was removed. Conversely, forest gains tended to occur where the gains did not create new forest interior, indicating that creation of forest interior was not usually an important consideration when forest was added. The dispersed and non-compensating patterns of forest losses and gains resulted in rates of net change of forest interior area that were at least 3 times larger than the rate of net change of total forest area. While the identity of forest interior is naturally scale-dependent, the multi-scale analysis showed that the non-compensating pattern of forest loss and gain was exhibited over a wide range of spatial scales from 4.41 ha to 5,310 ha.

Our estimates of the absolute amount of forest interior area are larger than estimates that define forest interior in terms of distance to nonforest conditions. The results of the distance approach must approximate the results of a comparably-scaled neighborhood approach when the forest interior criterion is taken to be $FAD = 1.0$. That is so because the maximum size neighborhood that contains only forest is necessarily related to the minimum possible distance to a non-forest pixel³². The use of a lower ($FAD \geq 0.9$) threshold value in this study resulted in the labeling of more of the extant forest area

as forest interior area in comparison to a higher threshold value²⁶, and therefore also in comparison to a comparably-scaled implementation of the distance approach. While the use of the distance approach would change the estimates of the absolute amount of forest interior area, it is unlikely that it would change the essential result that forest interior area was lost at a higher rate than total forest area over a wide range of spatial scales.

Trends of forest interior area are coarse-scale indicators of dependent ecological changes, yet the specific impacts of forest interior loss will naturally depend upon local circumstances such as the vegetation type experiencing the forest loss, the proximate causes of loss, and anthropogenic land uses in the vicinity. Our analysis did not distinguish between natural and anthropogenic loss and gain, nor did it compare conditions in 2001 with the patterns of potential natural vegetation absent human influences. Knowledge of potential natural vegetation is helpful for understanding specific impacts of fragmentation but it is not essential when evaluating trends of forest interior area within the human dominated era. More information is needed to evaluate quantitatively the relative importance of the causes of fragmentation in different parts of the United States. The principal drivers of forest area change appear to be human activities in the East and intense, yet relatively local (relative to the scale of the study area), biotic and abiotic disturbances in the West (see Supplementary Information online).

Sustainable natural resource stewardship must account for fluxes in the natural capital that provides the desired benefits^{4,13,14,33–36}. If the recent patterns of change continue, the extant forest interior area will become smaller and more concentrated on publicly owned land^{14,20,37}. As a result, sustaining the full range of benefits which depend on forest interior environments may become more difficult and fewer options may be available to natural resource managers. Land cover maps provide the synoptic perspective needed to identify indicators of forest interior consistently over large regions through time^{13,38}. In addition to total forest area, forest patterns could be monitored to better understand the impact of human activities on the sustainability of forest interior and subordinate ecological attributes and functions.

Methods

Land cover maps. Forest spatial patterns were measured on the 2001 and 2006 National Land Cover Database (NLCD) land cover maps^{29,30}. The NLCD land cover mapping protocols identify 16 land cover classes at a spatial resolution of 0.09 ha/pixel^{39–41}. For this analysis, the 16 NLCD land cover classes were combined into two generalized classes called forest (the NLCD deciduous, evergreen, mixed forest, and woody wetlands classes), and nonforest (all other NLCD classes). The overall per-pixel classification accuracy of forest versus nonforest was approximately 90% for the 2001 NLCD map⁴². Accuracy assessment of the 2006 map is underway and is expected to show a similar level of accuracy. Estimates of forest area from NLCD land cover maps differ from official United States forest area statistics⁴³ because of differences in the definition of forest and because official statistics consider land use instead of land cover. Areas of extra-territorial land and ocean water were treated as missing data, and forest area outside of the defined ecological sections⁴⁴ was not included in data summaries.

Forest interior analysis. Forest area density (FAD) is defined as the proportion of all NLCD land cover pixels within a fixed-area neighborhood that are forest. If forest is not fragmented in the vicinity of a given forest pixel, then by definition FAD equals 1.0 for a neighborhood which contains that forest pixel. On the other hand, if forest is fragmented in the vicinity, then the value of FAD is less than 1.0 in proportion to the degree of fragmentation (i.e., number of nonforest pixels) within the neighborhood. Thus, FAD is a simple metric of fragmentation as a contextual variable associated with a given forest pixel. Note that when preparing Fig. 1, except for the case of $FAD = 1.0$, the FAD values were grouped into 20 equal-width intervals represented by the midpoint values of 0.025, 0.075, 0.125, ..., 0.975.

To account for the scale-dependence of fragmentation, note that the value of FAD associated with a given forest pixel will increase or decrease with neighborhood size in proportion to changes in the degree of fragmentation at different spatial scales. A smaller neighborhood is more sensitive to fragmentation that varies at a higher spatial frequency, while a larger neighborhood is more sensitive to fragmentation that varies at a lower spatial frequency²⁶. In this analysis, we evaluated FAD at five measurement scales defined by neighborhood sizes equal to 4.41 ha (7 pixels X 7 pixels), 15.21 ha (13 X 13), 65.61 ha (27 X 27), 590.49 ha (81 X 81), and 5314.41 ha (243 X 243). Note that those neighborhood sizes were rounded to three significant digits elsewhere in



this report. Neighborhood shape is arbitrary, and neighborhood sizes were selected to represent several orders of magnitude of spatial scale.

A given forest pixel was labeled as “forest interior” at a given measurement scale if the associated FAD $\geq 0.9^{31}$. The threshold value is a tuning parameter in the sense that more or less of the extant forest will be labeled as forest interior as the threshold is lowered or raised²⁶. Very little forest area qualifies as forest interior for higher thresholds especially in larger neighborhoods, and almost all forest qualifies as forest interior with very low thresholds in smaller neighborhoods²⁶. For simplicity and comparability with earlier reports, we used a threshold value that has been commonly applied in other broad scale forest assessments in the United States^{14,45}. For a given neighborhood size, a map of forest interior at a spatial resolution of 0.09 ha/pixel comprised the subset of all extant forest pixels which met the criterion defining forest interior.

The following procedures were used to relate forest area gains and losses to the dynamics of forest interior area from 2001 to 2006. The NLCD forest maps from 2001 and 2006 were overlaid, on a pixel-by-pixel basis, upon the maps of FAD. Pixels that were forest in 2001 but not in 2006 represented forest area loss, and pixels that were forest in 2006 but not in 2001 represented forest gain. Pixels of forest loss were evaluated in relation to FAD in 2001 to determine whether forest area losses were also removing forest interior. Pixels of forest gain were evaluated in relation to FAD in 2006 to evaluate whether forest area gains were adding forest interior. The differences between gross gains and gross losses for FAD ≥ 0.9 represent the net changes of forest interior area.

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Author contributions

KHR and JDW designed research, KHR performed research and analyzed data, and KHR and JDW wrote and reviewed the manuscript.

Additional information

Supplementary information accompanies this paper at <http://www.nature.com/scientificreports>

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