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Exposure of Protected and Unprotected Forest to Plant Invasions in the Eastern United States

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Abstract: ***Research Highlights***: We demonstrate a macroscale framework combining an invasibility model with forest inventory data, and evaluate regional forest exposure to harmful invasive plants under different types of forest protection. ***Background and Objectives***: Protected areas are a fundamental component of natural resource conservation. The exposure of protected forests to invasive plants can impede achievement of conservation goals, and the effectiveness of protection for limiting forest invasions is uncertain. We conducted a macroscale assessment of the exposure of protected and unprotected forests to harmful invasive plants in the eastern United States. ***Materials and Methods***: Invasibility (the probability that a forest site has been invaded) was estimated for 82,506 inventory plots from site and landscape attributes. The invaded forest area was estimated by using the inventory sample design to scale up plot invasibility estimates to all forest area. We compared the invasibility and the invaded forest area of seven categories of protection with that of de facto protected (publicly owned) forest and unprotected forest in 13 ecological provinces. ***Results***: We estimate approximately 51% of the total forest area has been exposed to harmful invasive plants, including 30% of the protected forest, 38% of the de facto protected forest, and 56% of the unprotected forest. Based on cumulative invasibility, the relative exposure of protection categories depended on the assumed invasibility threshold. Based on the invaded forest area, the five least-exposed protection categories were wilderness area (13% invaded), national park (18%), sustainable use (26%), nature reserve (31%), and de facto protected Federal land (36%). Of the total uninvaded forest area, only 15% was protected and 14% had de facto protection. ***Conclusions***: Any protection is better than none, and public ownership alone is as effective as some types of formal protection. Since most of the remaining uninvaded forest area is unprotected, landscape-level management strategies will provide the most opportunities to conserve it.

Keywords: exposure; invasive species; forest; protected area; invasibility

1. Introduction

Protected areas such as parks and forest reserves are important components of natural resources conservation. Originally motivated to preserve unique or irreplaceable resources, protected areas later became the centerpiece of global strategies to conserve biodiversity while promoting other socio-ecological values such as sustainable development, carbon sequestration, and water quality [1].

As of 2009, 13% of the global terrestrial area was "formally protected" according to IUCN (International Union for Conservation of Nature) standards [2], of which approximately half had "strict protection for biodiversity" [3]. Giving areas protected status may be an efficient way to achieve many biodiversity objectives [4], but there is a continuing discussion of protection objectives, conservation targets, and the effectiveness of protected areas [5–9]. Nevertheless, it is necessary to understand what is threatening biodiversity in order to reduce the rate of biodiversity loss [10]. There is no doubt that attention must be given to the threats that degrade ecological integrity which is the foundation for biodiversity [2,11–13]. In North America, the call to manage whole landscapes to achieve biodiversity goals [14] has been answered by a public land management strategy to conserve ecological integrity—biodiversity writ large—on both protected and unprotected lands [15].

Estimating the actual exposure of protected areas to threats such as urban sprawl and climate change is foundational to developing effective management strategies [16]. Similarly, knowledge of exposure to invasive species is foundational because they by definition degrade the ecological integrity of natural communities, and furthermore they can cause significant and long-term modifications of ecosystems [17–21]. In a study of threats to 1961 terrestrial protected areas in 149 countries, invasive species were ranked as the fourth (of 45) most common type of threat [22]. Threats posed by invasive species are so important in the protected areas of the United States that invasive plant control has been implemented in almost every unit of the National Park System [23], and the National Park Service now monitors invasive plants as an indicator of biological integrity [24].

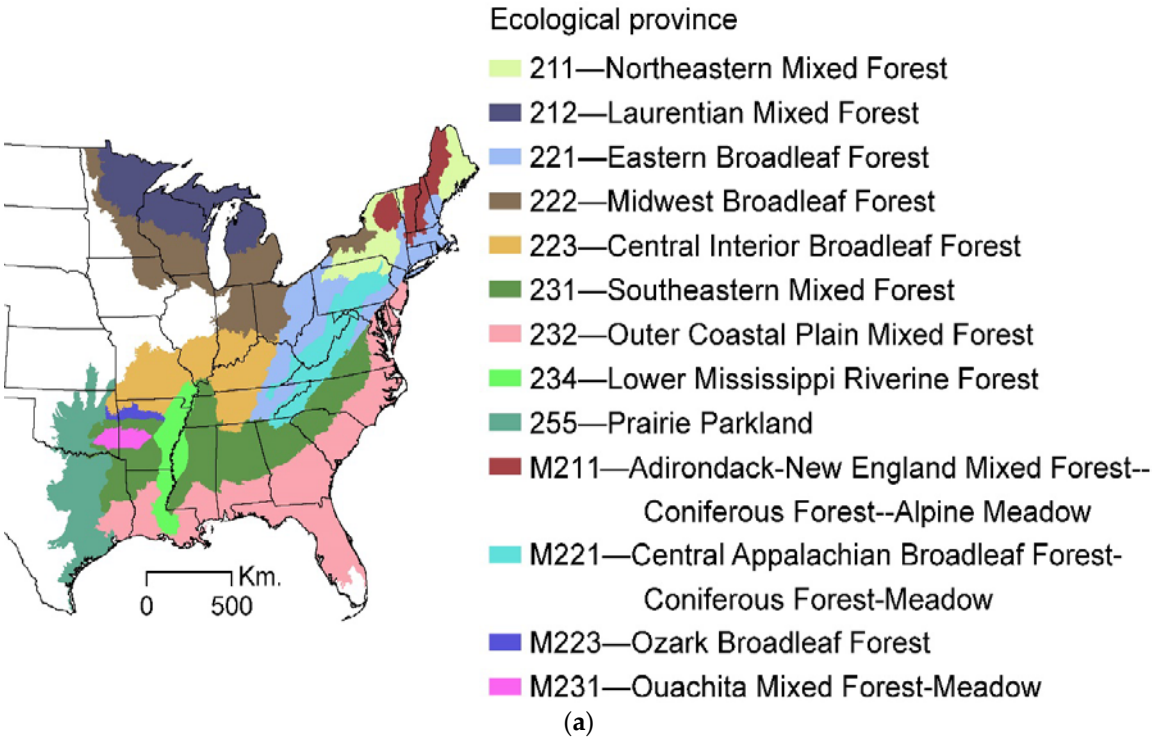
Regional assessments of invasive plants are difficult because jurisdictional and methodological differences lead to inconsistent measurements of exposure to invasive plant species over large areas incorporating all protected and unprotected areas. While remote sensing is useful for large-area assessments of some types of threats [10,13], exposure to invasive plant species is not one of them [22] and, as a result, consistent field sampling is required. In the United States, field observations made by the USDA (United States Department of Agriculture) Forest Service Forest Inventory and Analysis Program (FIA) can support consistent, national, and statistically valid estimates of forest exposure to invasive plant species across all types of protection status. Previous analyses of forest plant invasions using the FIA database [25–28] have yielded many insights but did not fully utilize the FIA sample design (see Supplementary Materials), and did not compare forest plant invasions in protected and unprotected areas.

Here we fully utilize the FIA sample design to evaluate the exposure of protected and unprotected forest to plant invasions across the eastern United States. Like earlier regional analyses based on GIS (geographic information system) extrapolation [29,30], our approach starts with a site-specific model of invasion. Invasibility (the probability that a forest site has been invaded) is estimated at the site level from plot and landscape (neighborhood) attributes. Unlike GIS extrapolation, which would require wall-to-wall mapping of model inputs, we scale up the model to the entire region using the FIA sample design. The invaded forest area is estimated using the area expansion factors from the sample design. This macroscale framework allows evaluation of the entire forest area in a consistent way while enabling comparisons of protection categories. Exposure to invasive plants is evaluated by comparing the invasibility and invaded area of IUCN protected forest with de facto protected (publicly owned) forest and unprotected forest. We included unprotected forest as a baseline for comparisons and to examine the possibility that landscape strategies involving privately owned lands may be useful to achieve conservation goals. Because plant invasions, land ownership, and protection status vary substantially across the study area, we also compared conservation opportunities in different ecological provinces.

2. Materials and Methods

The study area included approximately 303 Mha (million hectares) in the 13 ecological provinces [31,32] that comprise most of the temperate and boreal forest in the eastern United States (Figure 1a). The study area was once predominately forested, but almost all forest in the region has

been modified by humans and approximately 40% of the original forest area has been converted to other land uses [33]. Approximately three fourths of the forest area is privately owned [34], and invasive exotic forest plants occur on approximately one half of the sites which have been surveyed by FIA in the region [26,27].



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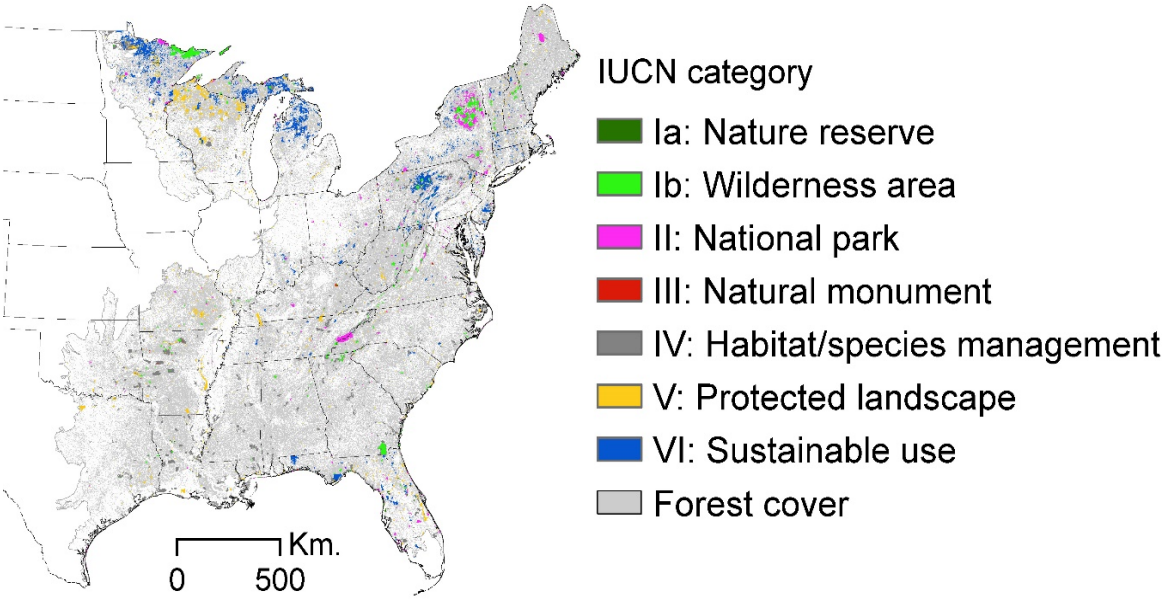

(**b**)

Figure 1. (**a**) Ecological provinces and study area; (**b**) IUCN protected areas and forest cover.

The FIA Program is an ongoing national census using a permanent, grid-based, equal probability sample design across all land with a sampling intensity of approximately one plot per 2400 ha of total area [35]. Field plots with a footprint of approximately 0.6 ha are established at sample locations where there is "forestland" (land that has, or has had, at least 10% tree crown cover, and is at least 0.4 ha in size and 37 m wide [36]). Forestland includes temporarily cleared land, but excludes tree-covered areas in agricultural production settings (e.g., fruit orchards) and in urban settings. We refer hereafter to forestland as "forest". The sample design has a target precision of $\pm 3\%$ for forest area estimates in the eastern United States. Each plot has an "expansion factor" that is calculated from the FIA sample design [35]; it is the area "represented" by that plot. For example, the total forest area is estimated by the sum of expansion factors for all forest plots. In 2001, FIA began observing invasive plants, defined as exotic plant species of any growth form that are likely to cause economic or environmental harm [37]. However, not all plots in the eastern United States have been surveyed for invasive plants. As a result, the surveyed plots do not by themselves constitute a statistical basis for regional comparisons of protected area effectiveness.

Instead, we conducted regional comparisons of exposure in a novel way by first estimating the invasibility of each plot, and then scaling up per-plot invasibility to regional estimates of invaded forest area using the FIA sample design. From the FIA database [38], we identified a set of 82,506 FIA plots that constituted a statistical basis for forest area estimation circa 2006. We modified an earlier model of invasibility [28] to estimate the probability that each of the plots had been invaded (see Supplementary Materials). Given an estimate of invasibility for a plot, the expansion factor for that plot estimates the area of forest with that invasibility. The regional estimate of the total forest area with a given invasibility is the sum of the expansion factors for all the plots with that invasibility. Since the per-plot product of invasibility and expansion factor estimates the invaded forest area represented by each plot, the regional estimate of invaded forest area is the sum of those products over all plots. Uninvaded forest area estimates are obtained by subtraction. Stratification is performed by defining subsets of plots (strata) and summing the areas within each subset.

We formed strata based on ecological provinces and protection categories. Each plot was assigned to an ecological province by overlaying the plot locations on the map of provinces (Figure 1a). A protection category was similarly assigned to each plot as follows (see also Supplementary Materials). If a plot was located within a polygon in the Conservation Biology Institute (CBI, Corvallis, OR, USA) database [39], then we used the CBI assignment of IUCN protection category (Figure 1b). IUCN protected area includes both publicly and privately owned land which meets specific criteria for category designation (see Supplementary Materials). If the CBI did not assign a protection category, then we used the ownership data from the forest inventory database to identify four additional protection categories: de facto Federal (public land managed by Federal agencies); de facto nonfederal (public land managed by State or local governments); unprotected family (private land owned by a family or an individual); and unprotected nonfamily (private land owned by a corporation, a non-governmental organization, or Native American entity).

To further assess invasibility differences among protection categories, we compared the cumulative invasibility, i.e., the cumulative percentage of forest area with invasibility less than a threshold value, among protection categories. This allowed us to evaluate differences in per-unit area exposures among protected categories for different invasibility thresholds. This perspective is useful for addressing conservation goals which are stated in terms of maintaining a minimum level of (rather than absence of) threat from invasive species [40,41]. In addition, since total forest area varies substantially among protection categories, we also compared the estimated proportion of total forest area that was invaded, i.e., total invaded forest area divided by the total forest area.

3. Results

The terrestrial protected area in all IUCN categories comprised approximately 20 Mha, which represents approximately 7% of the study area (Table 1). Approximately 11 Mha (4% of the study area) was in an IUCN category with strict protection for biodiversity (i.e., strictly protected area). Since protected areas contained non-forest land uses, our estimates of protected forest area (estimated by the FIA sample design) were naturally smaller than estimates of total protected area. We estimated that 16.1 Mha (10.3%) of the total 157.0 Mha of forest in the study area was protected according to IUCN standards (Table 2). Thus, forest occupied 80% of the total protected area in the eastern United States. The forest with strict protection for biodiversity amounted to 5% of total forest area, 52% of total protected forest area, and 76% of the total strictly protected area. For the forest that was not labeled by an IUCN category, we estimated that 123.7 Mha (88%) was privately owned and 17.2 Mha (12%) was publicly owned (Table 3). Family-owned forest comprised 69% of the unprotected privately owned forest, while 58% of the de facto protected forest was in Federal ownership.

Table 1. Total IUCN protected area.

Province	Total Area	Protected Area		Strictly Protected Area [1]	
	Mha [2]	Mha	% [3]	Mha	% [4]
211	13.6	1.3	9.7	0.6	42.1
212	25.8	5.8	22.3	1.3	22.5
221	26.4	1.2	4.7	0.7	55.6
222	36.7	1.3	3.4	0.8	60.5
223	31.0	1.0	3.2	0.5	51.9
231	47.0	1.1	2.3	0.9	81.5
232	55.6	3.6	6.5	2.5	68.6
234	10.9	0.6	5.9	0.5	73.6
255	24.6	0.3	1.4	0.2	70.8
M211	9.8	1.7	17.0	1.4	83.8
M221	16.9	1.8	10.5	1.3	71.7
M223	1.7	0.2	9.3	0.1	88.0
M231	2.9	0.3	10.6	0.3	87.0
All	302.8 [5]	20.2	6.7	11.0	54.5

[1] Strictly protected area includes nature reserve, wilderness area, national park, natural monuments or features, and habitat/species management areas [3] (see also Supplementary Materials); [2] Million hectares; [3] Percent of total area; [4] Percent of protected area; [5] Sums and percentages may reflect rounding errors.

Table 2. IUCN protected forest land area.

Province	Forest Land Area	Protected Area		Strictly Protected Area		Forest Share of:	
						All Protected Area	Strictly Protected Area
	Mha	Mha	% [1]	Mha	% [2]	%	%
211	9.9	1.3	12.7	0.5	42.3	94.0	94.5
212	17.1	4.6	27.1	0.8	18.1	80.3	64.3
221	14.2	1.1	7.6	0.5	50.3	87.3	78.9
222	7.0	0.7	9.7	0.4	50.9	53.8	45.3
223	12.9	0.8	6.3	0.4	48.3	81.5	75.8
231	29.4	1.0	3.3	0.8	81.7	86.9	87.2
232	32.9	2.5	7.6	1.6	64.6	68.8	64.8
234	3.0	0.5	15.6	0.4	79.0	71.9	77.2
255	6.8	0.2	2.3	0.1	72.1	46.7	47.5
M211	8.6	1.6	18.1	1.3	85.3	94.4	96.1
M221	11.9	1.6	13.8	1.2	71.9	91.6	91.9
M223	1.3	0.2	11.5	0.1	90.3	92.1	94.5
M231	2.3	0.3	12.5	0.3	89.0	92.8	94.9
All	157.0 [3]	16.1	10.3	8.4	52.1	79.9	76.5

[1] Percent of forest land area; [2] Percent of protected forest land area; [3] Sums and percentages may reflect rounding errors.

Table 3. Estimated exposure of forest area to invasive species. Categories are sorted by the proportion of total area invaded.

Protection Category	Estimated Forest Area	Estimated Invaded Forest Area		Estimated Uninvaded Forest Area
		Proportion	Absolute	
	Mha	%	Mha	Mha
Wilderness area	1.64	12.5	0.20	1.44
National park	1.59	18.1	0.29	1.31
Sustainable use	4.97	26.3	1.31	3.66
Nature reserve	0.18	31.0	0.06	0.13
de facto Federal	10.01	35.6	3.56	6.45
Protected landscape	2.76	36.7	1.01	1.75
de facto nonfederal	7.23	40.8	2.95	4.28
Habitat/species management	4.93	40.9	2.02	2.91
Natural monument	0.06	45.4	0.03	0.03
Unprotected nonfamily [1]	38.14	46.0	17.55	20.58
Unprotected family [2]	85.51	60.0	51.32	34.19
All protection categories	157.03 [3]	51.1	80.30	76.73

[1] Private, family-owned, no IUCN designation; [2] Private, not family-owned, no IUCN designation; [3] Invaded and uninvaded area my not sum to total forest area due to rounding.

Invasibility varied substantially among plots within a given protection category (Figure 2). Several examples will illustrate how to interpret cumulative invasibility in terms of relative exposure. For example, approximately 75% of forest in wilderness areas had invasibility less than 0.2, and 95% had invasibility less than 0.4. For an invasibility threshold of 0.4, wilderness areas were less exposed than all other categories because the percentage of forest in wilderness areas at that threshold was higher than for all other categories. Similarly, the nature reserve category was less exposed than the sustainable use category for invasibility thresholds up to 0.2, but the relative exposures of those two categories changed for larger invasibility thresholds. With the exception of the apparently least exposed (wilderness area) and most exposed (unprotected family) categories, the relative exposure of a protection category depended on the invasibility threshold. Overall, any type of protection was better than no protection, and, in some cases, de facto protection was better than some types of IUCN protection.

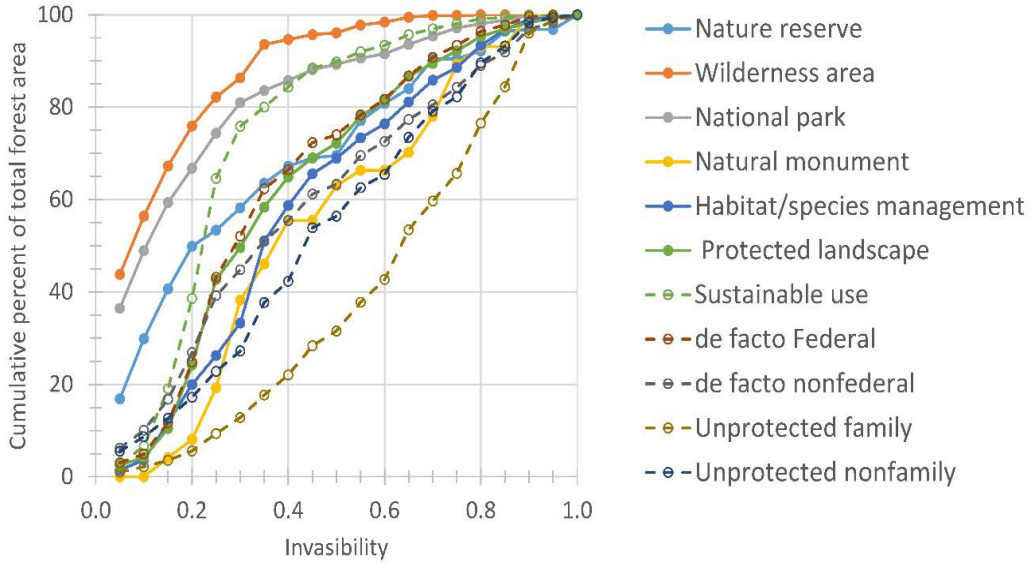

Figure 2. Estimated cumulative invasibility by protection category. Each point indicates the percentage of total forest area with invasibility less than or equal to the indicated value. Note: "unprotected family" is private, family-owned, no IUCN designation; "unprotected nonfamily" is private, not family-owned, no IUCN designation.

Assessing estimated cumulative invasibility permitted direct comparisons of protection categories but masked the large differences in total forest area among categories. Owing to both differences in invasibility and in total forest area, the invaded forest area varied substantially among protection categories (Table 3). Overall, we estimated that 80.3 Mha (51%) of forest in the region was invaded, of which 4.9 Mha (6%) was located in protected areas, 6.5 Mha (8%) occurred in forest with de facto protection, and 68.9 Mha (86%) was in unprotected areas. Of the 76.7 Mha (49%) of forest in the region which was uninvaded, 11.2 Mha (15%) was located in protected areas, 10.7 Mha (14%) occurred in forest with de facto protection, and 54.8 Mha (71%) was located in unprotected areas. Since the proportion of forest area invaded (Table 3) is essentially area-weighted mean invasibility, it subsumed threshold dependence (Figure 2) and allowed for comparisons of exposure over the full range of invasibility. This simpler format suggested that the least exposed protection categories were wilderness area (13% of total forest area invaded), national park (18%), sustainable use (26%), nature reserve (31%), and de facto protected Federal land (36%) (Table 3). The exposure of unprotected nonfamily forest was similar to the most exposed IUCN category (natural monuments), and the exposure of unprotected family forest was roughly five times larger than the least exposed protection category (wilderness area).

The opportunities for conferring IUCN protection upon uninvaded forest with de facto or no protection varied substantially among ecological provinces (Figure 3). The estimated de facto share of uninvaded forest was larger than the IUCN protected share in seven of the 13 provinces (223, 231, 232, 255, M221, M223, and M231) but was smaller than the unprotected share in all provinces. In all provinces except 234, M211, and M231, the largest share of uninvaded forest was unprotected family forest. The unprotected nonfamily category contained the second-largest share in all provinces except 212, 222, 223, and M223.

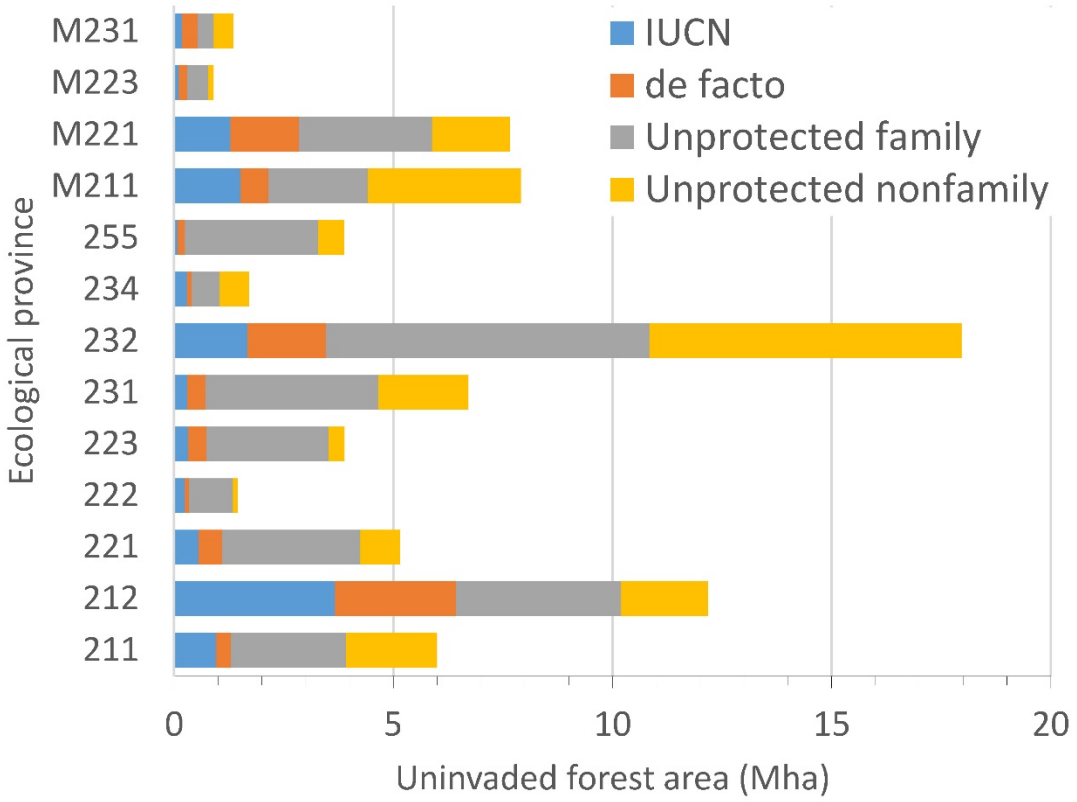

Figure 3. Estimated area of uninvaded forest by ecological province and protection category. IUCN includes all IUCN protection categories and de facto includes both Federal and nonfederal ownerships. Note: "unprotected family" is private, family-owned, no IUCN designation; "unprotected nonfamily" is private, not family-owned, no IUCN designation.

4. Discussion

In the eastern United States, forest plant invasions cannot be ignored when evaluating either the exposure of protected areas to ecological threats or the estimated capacity of protected and unprotected land to achieve the goal of conserving ecological integrity. Forest comprised 80% of the total protected area and invasive forest plants have already been found on more than half of all forest plots examined [26]. Our models estimated that 19% of protected forest had more than a 50:50 chance of having been invaded by harmful forest plants, while 31% had more than a one in three chance of being invaded. Invasibility was much higher on unprotected forest, where we estimated 57% had more than a 50:50 chance of being invaded, and 72% had more than a one in three chance. Forest with very low estimated invasibility (less than a one in 20 chance) was relatively rare, comprising only 10% of protected forest and 3% of unprotected forest. Our analysis was conservative because the data used to build the invasibility model did not consider all exotic or invasive plant species, only those determined by experts to cause economic or environmental harm [37].

In comparison to the global biodiversity target of protecting 17% of total area [7], our analysis estimated that two of the 13 provinces had more than 17% of both total area and forest area protected, but the percentages over the entire study area (6% and 10%, respectively) were less than the target (Tables 1 and 2). If all of the forest with de facto protection were to be accorded IUCN protection, then both total and forest protected areas would approximately double and the 17% target would be attained for forest but not for total protected area. In contrast to biodiversity targets, there are no established targets for invasibility, invaded forest area, or exposure to invasive forest plants. If such targets were to be identified, then our framework would provide estimates of whether the targets have been achieved under different types of protection and in different places.

To the extent that forest plant invasion by species known to cause economic or environmental harm is an indicator of ecological integrity, our estimated results for invasibility (Figure 2) and invaded forest area (Table 3) generally indicate that, in comparison to unprotected forest, protection has been effective for conserving ecological integrity. This conclusion was determined mainly by the apparent effectiveness of wilderness areas, national parks, and sustainable use areas. There was little evidence that the effectiveness of other IUCN protection categories (nature reserves, protected landscapes, habitat/species management areas, and natural monuments) differed substantially from the effectiveness conferred by public ownership (de facto protection), particularly Federal ownership. There was ample evidence that de facto protection has been effective in comparison to unprotected family forest.

It was surprising that the sustainable use protection category was estimated to have the third-smallest proportion of forest area invaded because those areas are nominally the least-protected IUCN category. In contrast to wilderness areas and national parks, the lower estimated exposure of sustainable use areas was not the result of a large area with low invasibility, but rather a large area with medium invasibility (Figure 2). The majority of the sustainable use land in the study area comprised publicly owned State forests (or their equivalent) in only a few States (Figure 1b). If that land had not been assigned an IUCN protection category, then it would have been included in a de facto protection category. Other de facto protected areas span a wide variety of management intensities, from those requiring management plans within which disturbance events are allowed to proceed without interference to those which allow either broad, low-intensity uses (e.g., logging) or localized high-intensity uses (e.g., mining). Such areas have protection of natural land cover for the majority of area, and confer protection to federally listed endangered and threatened species throughout the area [42]. While that language suggests "sustainable use", it is arguable whether the de facto protected area achieves, or simply resembles the management objectives of the IUCN sustainable use category. In any case, most of the de facto protected forest in the eastern United States comprises National Forest System general public lands, State forests, and game sanctuaries where minimizing the occurrence of invasive plant species is likely to be a management goal.

We believe that the apparently superior conditions found in wilderness areas, national parks, and sustainable use areas were the result of remoteness rather than protection per se [28,43]. The invasibility model predicted the lowest invasibility for forest plots with low productivity that were not near roads and were in unfragmented neighborhoods without intensive human land uses (see Supplementary Materials). Forest area meeting those criteria was relatively rare and was mostly contained within a few large wilderness areas, national parks, and sustainable use areas (Figure 1b) where cold temperature, steep terrain, and/or water limited the occurrence of farms, urban areas, and roads. Furthermore, the relatively large size of such areas implied a certain degree of remoteness at least in the core area which has been buffered from invasions from adjacent areas. Whether driven by protection or by remoteness, it remains that the exposure of these areas is now relatively low. Protection is still important because removing protection would ultimately reduce the remoteness of these areas through the creation of new roads, housing, and associated infrastructure, which is likely to lead to increased exposure in these forested landscapes.

The finding that nature reserves did not have exceptionally low estimated exposure was also surprising. Such areas are intended to provide "indispensable reference areas for scientific research and monitoring" [2]. The estimated invasibility of such forest suggests that more than 60% of the forest area had more than a 50:50 chance of having been invaded (Figure 2), and we estimated that almost one-third of the forest area was invaded (Table 3). It is therefore questionable that such areas can provide a useful reference for long-term plant community studies. Given those conditions in nature reserves, it is possible that only large national parks or wilderness areas can provide large tracts of uninvaded reference conditions, but those conditions exist in only a few parts of the study area. Similarly, the relatively high estimated exposures of natural monuments and habitat/species management areas to invasive plants call into question their inclusion among the IUCN categories with strict protection for biodiversity.

The differences in estimated total invaded and uninvaded areas for different protection categories were driven primarily by differences in total forest area rather than by differences in estimated invasibility. Despite having the highest estimated exposure in terms of cumulative invasibility and proportion of forest area invaded, unprotected forest still had the largest estimated share of uninvaded area because most of the total forest area was unprotected. Similarly, protected forest generally had lower estimated exposures but comprised a smaller share of uninvaded forest area simply because most of the total forest area was not protected. This strengthens the argument for conservation strategies which consider whole landscapes including areas allocated to both production and protection [14,44,45]. The efficacy of restoring invaded sites is uncertain [46] and the protection of natural communities from invasive plants may not be a central management objective for many protected areas (e.g., battlefield parks). If the alternative is conservation by preservation, then a conservation strategy incorporating privately owned forest has the largest area of uninvaded forestland to work with.

Efforts to take advantage of that opportunity naturally lie within the private sector, where there are important socio-economic obstacles [47]. If exposure is attributable to remoteness rather than protection per se, then a strategy based on unprotected family forest will involve adjacent landowners acting in concert, in order to conserve a relatively remote condition. Furthermore, many landowners may be involved because the average forest parcel size is only ~50 ha in the eastern United States [48]. It may be easier to confer additional protection upon relatively remote public lands with larger parcel sizes, but additional protection per se may not matter if the relative remoteness of that land is not maintained. We expect conditions may be much different in the western United States, where there are many protected areas which are quite large [39] and where the historical rate of forest plant invasions is lower [27].

In a discussion of the addition of the protected landscape and sustainable use categories to the IUCN classification system, it has been argued that assigning conservation recognition to such relatively low-quality land will devalue conservation biology and undermine the creation of more strictly protected area [49]. The counter-argument is that on-the-ground management may be more

important than global classification schemes for determining the effectiveness of protected areas [50]. While our results are for the eastern United States where human influences are already pervasive, they tend to support the latter view. In this region, there are not many opportunities for creating new protected areas in pristine condition, and de facto protection may be at least as effective as formal protection for achieving some conservation objectives. The control of biological invasions is most effective when it employs a system-wide strategy [18], and it follows that conservation planning in the face of invasions must also adopt an approach that considers the portfolios of both protected and unprotected areas within a landscape context.

5. Conclusions

We developed a macroscale framework to evaluate the exposure of protected and unprotected forest to invasive plants. The framework was built upon a site-level invasibility model and the nationwide forest inventory system to provide consistent estimates at regional scale. Any protection was better than none, and public ownership alone was as effective as some types of formal protection. Since most uninvaded forest area was unprotected, landscape-level management strategies will provide the most opportunities to conserve it. Follow-up investigations would naturally be needed to address management plans for specific locations within the region. Invasive plant occurrence is only one aspect of ecological condition, but our assessment framework can be used to assess any other aspect of which can be calculated directly from the forest inventory database, or attributed to plot locations by geographic overlay, or estimated for plot locations.

Supplementary Materials: The following are available online at http://www.mdpi.com/1999-4907/9/11/723/s1, Supplementary methods S1: Assignment of protection categories to plots, Supplementary methods S2: Invasibility model.

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