ENVIRONMENTAL LAW & POLICY CENTER

June 1, 2026

Submitted via Email

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ATTN: Ginger Molitor
U.S. Forest Service, Great Divide Ranger District
10650 Nyman Avenue
Hayward, WI 54843

Re: Comments on the Environmental Assessment for the Chequamegon-Nicolet National Forest's West Zone Aspen Fir Regeneration Project

Dear Forest Supervisor Crocker:

The Environmental Law & Policy Center and Friends of the Yellow River are submitting these comments on the U.S. Forest Service's proposed West Zone Aspen Fir Regeneration Project in the Chequamegon-Nicolet National Forest. The proposed project would clearcut over 45,000 acres of forest, resulting in significant adverse impacts on the environment. The Forest Service asserts that this project is "needed to meet the LRMP objective for sustainable timber production that is critical to the nation's well-being and needs pursuant to Executive Order (EO) 14225, Immediate Expansion of American Timber Production."[1] Under the National Environmental Policy Act, the agency cannot move forward with logging at such a scale without thoroughly evaluating the project's reasonably foreseeable impacts and assessing a reasonable range of alternatives in an environmental impact statement.[2] The Forest Service's use of an environmental assessment is accordingly arbitrary and unlawful. The agency has also arbitrarily analyzed only one resource category and disregarded most of the project's environmental impacts. And rather than considering a reasonable range of alternatives, the Forest Service has unlawfully focused only on its proposal and a no-action alternative.[3] To comply with NEPA, the Forest Service must prepare a full EIS which includes a thorough evaluation of all significant environmental effects and a consideration of a reasonable range of alternatives.

[1] U.S. Forest Serv., Chequamegon-Nicolet National Forest, West Zone Aspen Fir Regeneration Project: Environmental Assessment and Finding of No Significant Impact (April 2026) ("West Zone EA"), at 7.

[2] *See* 42 U.S.C. § 4332(2)(C), (H).

[3] West Zone EA at 31-40; *see also id.* at 28 (analyzing only a "no action" alternative).

I. The significant effects of the West Zone Aspen Fir Regeneration Project must be thoroughly considered in an environmental impact statement.

At the center of NEPA's action-forcing scheme is the EIS. In the words of the statute, every federal agency must "include in every recommendation or report on … major Federal actions significantly affecting the quality of the human environment, a detailed statement" addressing five fundamental issues:

> (i) [the] reasonably foreseeable environmental effects of the proposed agency action;
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> (ii) any reasonably foreseeable adverse environmental effects which cannot be avoided should the proposal be implemented;
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> (iii) a reasonable range of alternatives to the proposed agency action, including an analysis of any negative environmental impacts of not implementing the proposed agency action in the case of a no action alternative, that are technically and economically feasible, and meet the purpose and need of the proposal;
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> (iv) the relationship between local short-term uses of man's environment and the maintenance and enhancement of long-term productivity; and
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> (v) any irreversible and irretrievable commitments of Federal resources which would be involved in the proposed agency action should it be implemented.[4]

These requirements were recently reaffirmed by Congress. The Fiscal Responsibility Act of 2023 directs each federal agency to "issue an environmental impact statement with respect to a proposed agency action requiring an environmental document that *has a reasonably foreseeable significant effect* on the quality of the human environment."[5] Congress emphasized that EAs are sufficient only when "a proposed agency action … does not have a reasonably foreseeable significant effect on the quality of the human environment[.]"[6]

Regarding the preliminary decision of whether an EIS is required, the Forest Service's regulations require the agency to "consider and analyze" both the "potentially affected environment" and the "degree of the effects of the action" when making a significance determination.[7] "Potentially affected environment" means "the condition of the physical,

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[4] 42 U.S.C. § 4332(2)(C).

[5] *Id*. § 4336(b)(1) (emphasis added).

[6] *Id*. § 4336(b)(2).

[7] 7 C.F.R. § 1b.2(f)(3) (effective July 3, 2025).

biological, social, and economic factors that may be impacted by an action."[8] And "[i]n considering the degree of effects," the agency should evaluate "the following, as appropriate to the specific action and in the context of the potentially affected environment: (A) Both short- and long term effects[;] (B) Both beneficial and adverse effects[;] (C) Effects on public health and safety[;] (D) Economic effects[;] [and] (E) Effects on the quality of life of the American people."[9]

Here, the Forest Service disregarded relevant factors the agency is required to evaluate under NEPA. Despite the Forest Service's own definition of significance, the agency failed to fully evaluate and disclose the magnitude of this proposal. The West Zone project would have significant environmental effects, including several foreseeable impacts that the Forest Service's assessment disregarded. The agency must accordingly evaluate the project's implications in a full environmental impact statement that considers a full range of reasonable alternatives. The decision to forego preparation of an EIS was arbitrary and unlawful.

A. Clearcutting 45,826 acres of the CNNF will have clear and significant effects that must be analyzed in an EIS.

The West Zone project, as proposed, would span a 45,826-acre area, the entirety of which would be clearcut over a 15-to-20-year period.[10] Logging cannot occur at such a scale without causing significant environmental effects in the short and long term.[11] The Forest Service's prior determinations in the CNNF confirm this. The Forest Service has repeatedly prepared EISs for proposed timber harvests involving significantly fewer overall acres and fewer acres of clearcutting.[12] For example, in 2018, the Forest Service prepared an EIS before approving the Townsend Project, which proposed to harvest 18,474 acres of timber with only 157 acres of clearcutting, in order to "disclose the potential consequences of implementing the Proposed Action and alternatives to that action so that the responsible official, the District Ranger, can make an informed decision."[13] The West Zone project would involve logging at a much greater

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[8] *Id.* § 1b.2(f)(3)(i).

[9] *Id*. § 1b.2(f)(3)(ii).

[10] West Zone EA at 22.

[11] *See* 7 C.F.R. § 1b.2(f)(3)(ii).

[12] *See*, *e.g.*, U.S. Forest Serv., Final Environmental Impact Statement, Lakewood Southeast Project, p. 6, 9 (Aug. 2013) (preferred alternative involved 10,751 acres of timber harvesting and 2,201 acres of clearcutting); U.S. Forest Serv., Final Environmental Impact Statement, Park Falls Hardwoods, p. xvii (Sept. 2012) (preferred alternative involved 17,024 acres of timber harvesting and 449 acres of clearcutting); U.S. Forest Serv., Final Environmental Impact Statement, Phelps Vegetation and Transportation Management Project, p. 23 (July 2011) (preferred alternative involved 8,433 acres of timber harvesting and 319 acres of clearcutting); U.S. Forest Serv., Final Environmental Impact Statement, Honey Creek-Padus Project, p. 30 (May 2010) (preferred alternative involved 6,702 acres of timber harvesting and 612 acres of clearcutting).

[13] U.S. Forest Serv., Final Environmental Impact Statement, Townsend Project, p. 4, 6 (Mar. 2018).

scale—with over 45,000 acres subject to clearcutting—than the Townsend Project. An EIS is clearly warranted here and the agency's conclusion to the contrary was arbitrary.

B. The Forest Service's own characterizations of the West Zone project and its foreseeable effects confirm the need to prepare an environmental impact statement.

Clearcutting and Vegetation Impacts. Studies cited by the Forest Service show the detrimental effects of clearcutting and indicate that significant impacts would result from the West Zone project. For example, the EA notes that there is "[e]cological evidence regarding the detrimental effects of clearcut management in adjacent forested lands, especially to understory plants and lichens … [and these effects include] increased air and soil temperature, solar radiation and light levels, wind speeds, and decreased humidity [which can make] previously suitable rare plant habitat unsuitable."[14] While the Forest Service recognized these inherent risks to sensitive plant species, it stated that the removal of stands from the project or the splitting of several aspen stands during development would be able to "avoid or mitigate impacts on rare plants on known or suitable rare plant habitat."[15] But this conclusion does not explain how and to what extent mitigation of the environmental harm would be achieved—something that must be evaluated by the agency in an environmental impact statement.

The Forest Service also proposes surpassing the typical 40-acre stand limit for clearcutting but does not provide the requisite rationale to receive an exemption from this requirement. When the Forest Service proposes "clearcutting, seed tree cutting, shelterwood cutting, or other cuts designed to regenerate an even-aged stand of timber, the plan must include standards limiting the maximum size for openings that may be cut in one harvest operation," and the limit for this forest type is 40 acres.[16] The EA notes that there will be numerous stands cut that are greater or equal to 40 acres including: 34 in the Great Divide Ranger District, 50 in the Medford-Park Falls Ranger District, and 15 in the Washburn Ranger District.[17] To receive an exemption from this baseline requirement, "the responsible official [must] determine[] that larger harvest openings are necessary to *help achieve desired ecological conditions in the plan area*."[18] The EA argues that this exemption is necessary "to regenerate large contiguous blocks of aspen and balsam fir to create early successional patches and bring age class distribution closer to LRMP desired conditions," and that "[l]imiting the size of temporary openings would create more edge habitat, fragmented stands would occur, and fewer acres would be converted to early successional growth, making it more difficult to maintain the correct percentages of these communities."[19] But the mere necessity of an exemption from this underlying protective standard

[14] West Zone EA at 27.

[15] *Id.* at 28.

[16] 36 C.F.R. § 219.11(d)(4).

[17] West Zone EA at 29, Table 7.

[18] 36 C.F.R. § 219.11(d)(4)(i) (emphasis added).

[19] West Zone EA at 30.

to limit clearcutting confirms that the agency needs to further analyze the significant impacts that would result from clearcuts of greater than 40 acres.

Transportation. According to the EA, there would be a significant increase in new and augmented existing roads under the West Zone project, including: "[a]pproximately 123 miles of NFS roads … added [and] … [o]f these 123 miles, 4 miles are new road construction"[20]; "approximately 73 miles [of temporary road construction] to provide access to timber harvest areas"[21]; and "approximately 61 miles of [road reconstruction on] existing system roads in the project area."[22] These roads would have significant adverse effects on the surrounding environment. The Forest Service recognizes the type of artificial alterations that will occur, but it arbitrarily does not analyze the associated environmental impacts from such alterations. For example, for road reconstruction specifically, the Forest Service states that the "[r]econstruction includes clearing and grubbing; reconditioning and improving the surface; constructing drainage dips, culverts, riprap fills, or other drainage or stabilization features with potential disturbance outside of the established road (toe of fill to top of cut); replacing stream crossings; realigning the road; widening the road to accommodate vehicles and logging equipment; and widening curves, as needed, to accommodate off-tracking of log trucks and other equipment. Reconstruction also includes the actions described in the maintenance category, including removal of roadside hazard trees."[23] Despite this long list of potential activities, the Forest Service has not analyzed the adverse environmental impacts that would foreseeably result from them. In terms of practical mitigation measures, the EA itself only mentions in passing that "[s]ome road reconstruction would occur in the winter to prevent soil compaction."[24] The EA fails to state, however, which roads this would apply to. Furthermore, the measure is not even carried over as-is into Appendix D—Standards, Guidelines, and Design Features—where the formal list of mitigation measures is provided. Appendix D includes a more lenient measure that allows the operation "of heavy equipment only when soils are not saturated or when the ground is frozen."[25] The sheer amount of road building and associated activity suggests that significant adverse environmental impacts could be inflicted on wetlands, species, habitat, and other resources.

Water Resources. The EA does not substantively address adverse effects to water resources. However, a small section in Appendix C notes that "[o]verall water quality for the wetlands, streams, lakes, and rivers in the project area is very good and considered pristine in

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[20] *Id.* at 23.

[21] *Id.* at 24.

[22] *Id*.

[23] *Id*.

[24] *Id*.

[25] U.S. Forest Serv., Chequamegon-Nicolet National Forest West Zone Aspen Fir Regeneration Project, Appendix D – Standards, Guidelines and Design Features Specifically Listed in Resource Analysis ("App. D.") at D-7, G-19.

some areas."[26] Furthermore, the Forest Service acknowledges that "[m]ost wetlands in the project area are intact, unmodified, and functioning highly."[27] Additionally, the Forest Service notes that "[s]treams in the project area contain high-quality habitat and are in free-flowing condition."[28] Given this overview, the Forest Service has made clear in this supplementary Appendix that there are important water resources in the project area. The Forest Service also recognized the risk this project poses to these resources when it found that "[p]roposed activities have the potential to affect water quality in the nine project area Hydrologic Unit Code (HUC) 8 watersheds (Figure C-1) by increasing sedimentation and temperature."[29] Despite this risk, the EA does not provide analysis of impacts under the assumption that "[t]he effect on water resources from proposed activities is not expected to impair the long-term water quality if BMPs are implemented correctly to minimize impacts on soils, wetlands, floodplains, and the watershed."[30] This arbitrarily ignores potential short-term impacts. And the Forest Service's reliance on BMPs does not exempt the agency from identifying impacts, analyzing them, and explaining how and to what extent the mitigation will be effective. NEPA requires that "mitigation be discussed in sufficient detail to ensure that environmental consequences have been fairly evaluated."[31] The Forest Service must do this in an EIS. And it must address the possibility that BMPs will not be fully implemented on the ground, as the Forest Service's own BMP monitoring often identifies implementation failures.

Listed Species. The Forest Service recognized adverse impacts to both threatened and endangered species, but still concluded that these impacts would not constitute a significant effect under NEPA. This was arbitrary. Species impacts which would result from this project are significant and should be considered in an EIS.

The Northern Long-Eared Bat. The Forest Service, in a separate Biological Evaluation, found that this project was "likely to adversely affect" the northern long-eared bat as there was "[s]uitable habitat for the species … present in the project area, and the bat has been confirmed to occur."[32] The bats use habitat in the project area to roost, and the project could remove habitat.[33] The Forest Service confirmed that "potentially occupied roost trees could be cut during

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[26] U.S. Forest Serv., Chequamegon-Nicolet National Forest West Zone Aspen Fir Regeneration Project, Appendix C – Other Issues and Other Law, Regulation, and Policy Consistency ("App. C") at C-15.

[27] *Id.*

[28] *Id*.

[29] *Id*.

[30] *Id*.

[31] *Robertson v. Methow Valley Citizens Council*, 490 U.S. 332, 352 (1989).

[32] U.S. Forest Serv., Biological Evaluation for the West Zone Aspen Fir Regeneration Project in the Chequamegon-Nicolet National Forest ("BE"), p. 22 Table 4 (April 2026).

[33] *See* BE at 28.

the summer occupancy period and pup season when young bats are unable to fly."[34] The impacts of this should be addressed in an EIS.

The Tri-Colored Bat. The Forest Service similarly found that this project was "[l]ikely to [a]dversely [e]ffect" the tri-colored bat and that there was "[s]uitable habitat for the species … in the project area."[35] The agency found that "[t]hese bats are commonly found in man-made structures as well as trees, caves, and rock crevices, and primarily roost among live and dead leaf clusters of live or recently dead deciduous hardwood trees."[36] The Forest Service also concluded that roost habitat for the Tri-Colored Bat could be removed by the project.[37]

Despite these findings regarding bat species pursuant to the Endangered Species Act, the Forest Service did not follow-up on these risks as part of its duty to evaluate species impacts in an EIS under NEPA.[38] This was arbitrary. Even if the Forest Service assumed that mitigation measures would reduce the impacts to a sufficient degree,[39] this falls short of what NEPA requires.[40]

According to the Forest Service's own analysis, the mitigation measures at issue may not even be effective. In fact, the agency found that "snag retention standards and reserve islands would not fully mitigate effects on roost tree availability. Cut stands would remain unsuitable to most bats for roosting purposes for at least 15 years following treatment implementation due to the time needed for sufficient complexity and size to develop in treated stands."[41] Therefore, the Forest Service's reliance on such measures to support a FONSI was arbitrary.

The Monarch Butterfly. The Forest Service found suitable monarch habitat in the project area, including grasslands, milkweed, and nectar sources.[42] Additionally, the Forest Service recognized that "[r]oad maintenance, including road brushing, may have adverse effects on monarch butterfly larvae."[43] This must be evaluated in an EIS.

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[34] *Id*. at 29.

[35] *Id*. at 23, Table 4.

[36] *Id.*

[37] *Id.* at 28.

[38] West Zone EA at 45.

[39] *See* BE at 29 ("[d]ue to LRMP standard and guidelines and BCS conservation measures, impacts on the species would be minimized").

[40] *See Robertson v. Methow Valley Citizens Council*, 490 U.S. 332, 352 (1989) (mitigation analysis must be detailed enough such that environmental consequences are evaluated).

[41] BE at 30.

[42] *See* BE at 23, Table 4.

[43] *Id.* at 26.

The Salamander Mussel. The agency found that this species may occur downstream from the project area[44] and the project has "the potential to cause sedimentation to streams."[45] Again, the Forest Service relied upon the claim that "implementation of design features [would] reduce sedimentation to levels that would result in no impacts on water quality in potential habitat."[46] The only corresponding BMP identified in Appendix D was the direction to "[u]tilize the *Wisconsin Construction Site Best Management Practices Handbook* as well as the *Best Management Practices for Erosion and Sedimentation Control* (Federal Highway Administration 1995) for guidance on limiting sedimentation."[47] This BMP does not reference a specific practice or location to implement it in the project area to protect the Salamander Mussel. The Forest Service's analysis was accordingly arbitrary.

The Gray Wolf. The Forest Service noted that "[s]uitable habitat for the gray wolf is present in the project area."[48] Additionally, the agency noted that "there would be an increase in human disturbance from harvesting and road work in the project area…."[49] The Forest Service did not analyze how this human disturbance could adversely affect the region's wolves, which was arbitrary under NEPA.

Sensitive Species. In addition to listed species, the Forest Service identified many Regional Forester Sensitive Species ("RFSS") that could be harmed by the proposal. The Forest Service found "five rare terrestrial vascular plant species … [that] have suitable habitat potential in the project area, all of which are listed as RFSS. Of these five species, four have confirmed presence within 0.25 mile of the project area, and one has suitable habitat but has not been documented in the project area to date."[50] Two of these, Bog bluegrass and the Lesser round-leaved orchid, may be adversely impacted by the project.[51] For both species, the Forest Service again argued that impacts would be mitigated by standards, guidelines, and design features.[52] As noted above, the Forest Service must analyze impacts further in a full EIS before concluding that mitigation guidelines will sufficiently negate adverse impacts.

For all the following species, the Forest Service found that the project "may adversely impact individuals or habitat but will not likely contribute to a trend toward federal listing or loss of viability to the population or species":[53]

- Black-backed woodpecker

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[44] *Id.* at 23, Table 4.

[45] *Id.* at 31.

[46] *Id*.

[47] App. D. at D-12, G-2.

[48] BE at 22, Table 4.

[49] *Id.* at 24-25.

[50] App. C at C-3.

[51] *Id.* at C-4 – C-5, Table C-3.

[52] *See id*.

[53] *Id* at C-6 – C-7, Table C-5.

- Connecticut warbler
- Red-shouldered hawk
- Spruce grouse
- American marten
- Big brown bat
- Little brown bat
- Wood turtle[54]

The Forest Service failed to adequately analyze the proposal's potential impacts on these species. It must do so in an EIS.

II. The Forest Service must address in a full EIS many issues and impacts that the EA ignored.

A. A full EIS must address more than just scenic impacts.

The Forest Service "identified scenery management as an issue to be analyzed in detail in this EA,"[55] but did not conduct deeper analysis of any other resource category. Again, the agency is required to identify the "reasonably foreseeable environmental effects of the proposed agency action [and] any reasonably foreseeable adverse environmental effects which cannot be avoided should the proposal be implemented."[56] The Forest Service claims that the only issue worth studying in this EA is scenery management, but as discussed above, water resources, soil, species, and vegetation should have been analyzed in the EA as well. The failure to do so was arbitrary and unlawful.

B. The Forest Service did not adequately analyze regeneration

The EA relies on purported failures of natural regeneration to support its goal to pursue artificial clearcutting. The Forest Service notes that the purpose of the project "is to shift stands containing aspen (*Populus* sp.) and balsam fir (*Abiesbalsamea*) in the project area to desired conditions."[57] In order to do this, the Forest Service claims "there is a need to regenerate large contiguous blocks of aspen and balsam fir to create early successional patches and bring age class distribution in line with LRMP.…"[58] In evaluating scenic impacts, the Forest Service concluded that "[w]ithout planned regeneration or treatments to maintain a mix of age classes, the scenic character of the project area may become less visually diverse and less aligned with the scenic objectives associated with these SIO settings and reduce visual variety for CNNF recreational users."[59] To achieve these goals, the Forest Service concluded that clearcutting was the best method; however, it has not considered the threat that clearcutting can create excessive deer grazing and therefore pose a threat to these regeneration goals. Research in nearby areas has

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[54] *See id*.

[55] West Zone EA at 9.

[56] 42 U.S.C. § 4332(C).

[57] West Zone EA at 7.

[58] *Id*.

[59] *Id.* at 36.

demonstrated that white-tailed deer have consistently depressed forest regeneration for decades with heavy cumulative effects across the region.[60] Given this very real threat, the West Zone project promises to make the regeneration problem worse not better.

The agency noted that "[c]omments regarding impacts of the Proposed Action on ungulates and potential browsing pressure on vegetation were received during the scoping period...." [61] The Forest Service knew that "[r]egeneration of aspen would create quality browsing habitat for ungulates since openings large enough to provide sufficient sunlight can offer dense grass and herbaceous growth … [and even recognized that] … [i]ncreased herbivory of desired conifer regeneration in adjacent stands may increase as a result of the Proposed Action, which may threaten regeneration of conifers and other lowland species."[62]

During the scoping process other commenters showed that "[c]learcutting thousands of acres of aspen, especially stands > 40 acres, will create a massive, temporary localized pulse of high-quality deer and elk forage (aspens suckers, other early successional browse). This will attract and potentially support higher localized densities of ungulates, concentrating them on the landscape. The subsequent intense browsing pressure on adjacent stands can jeopardize the survival of any existing or future white pine, hemlock, or cedar regeneration, effectively sterilizing these areas from the very species the LRMP guideline aims to protect."[63] In response, the Forest Service asserted that "harvesting would be implemented over 15 to 20 years in two phases to limit the amount of large temporary openings at one time and minimize the effect of the Proposed Action on herbivory and ungulates."[64] This response does not adequately address the issue because it neither (1) provides any supporting analysis of the actual potential impacts of deer grazing nor (2) addresses how deer grazing could jeopardize the purported purpose of the project in the first place. The agency must adequately address this issue in an EIS now.

III. In preparing its environmental impact statement, the Forest Service must consider a reasonable range of alternatives that include additional resource protections.

The deficiencies of the EA are not limited to a lack of analysis of the proposed project's environmental impacts. The EA also fails to evaluate a reasonable range of alternatives—a problem that must be remedied in the Forest Service's EIS. Under NEPA, an agency's environmental review must consider "a reasonable range of alternatives … that are technically and economically feasible, and meet the purpose and need of the proposal[.]"[65] These options have to include "appropriate alternatives to recommended courses of action in any proposal

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[60] Bradshaw, L., and D.M. Waller. *Impacts of white-tailed deer on regional patterns of forest tree recruitment*, Forest Ecology and Management. 375: 1-11 (2016) (attached).

[61] App. C at C-10.

[62] *Id*. at C-11.

[63] U.S. Forest Serv., Chequamegon-Nicolet National Forest West Zone Aspen Fir Regeneration Project, Appendix B – Public Scoping Comments and Response, Issue Code 3045, Doc ID; 0007-6

[64] *Id*.

[65] 42 U.S.C. § 4332(C)(iii).

which involves unresolved conflicts concerning alternative uses of available resources[.]"[66] In this instance, the Forest Service simply analyzed the proposed project and the no-action alternative. This is inadequate, and "[i]f NEPA mandates anything, it mandates this: a federal agency cannot ram through a project before first weighing the pros and cons of the alternatives."[67] The Forest Service is doing just that.

Pursuant to 7 C.F.R. § 1b.5(c)(2)(ii), an EA may proceed without consideration of additional alternatives only where there are no unresolved conflicts regarding the proposed action.[68] This proposed project involves numerous unresolved conflicts, however, including:

1) The appropriateness of the Forest Service's plan to authorize widespread clearcutting in the CNNF, which will prevent the targeted areas from naturally transitioning to mature stands and old growth.
2) The Forest Service's failure to adequately address the deer grazing issue, which threatens the purported purpose of the project.
3) The Forest Service's failure to adequately analyze any other resource category aside from scenic impacts.
4) The Forest Service's continued reliance on mitigation measures to support its finding of no significant impacts to a broad range of resource categories.
5) The Forest Service's claim that more than 45,000 acres of clearcutting only requires cursory analysis in an EA.

The lack of alternatives analysis here is in violation of NEPA. The Forest Service should move forward with a thorough alternatives analysis in an EIS to remedy this.

IV. Conclusion

The West Zone Aspen Fir Regeneration project would have significant and unlawful effects on the lands and wildlife of the Chequamegon-Nicolet National Forest. The Forest Service must accordingly prepare an environmental impact statement evaluating lawful alternatives that would better protect the forest's extraordinary resources. We would welcome the opportunity to work with the agency as it moves forward with this process.

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[66] *Id*. § 4332(H).

[67] *Simmons v. U.S. Army Corps of Eng'rs*, 120 F.3d 664, 670 (7th Cir. 1997).

[68] 7 C.F.R. § 1b.5(c)(2)(ii).

Sincerely,

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Forest Ecology and Management 375 (2016) 1–11

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Impacts of white-tailed deer on regional patterns of forest tree recruitment

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ARTICLE INFO

Article history:
Received 16 March 2016
Received in revised form 9 May 2016
Accepted 13 May 2016
Available online 20 May 2016

Keywords:
USFS FIA data
Tree demography
Tree regeneration
White-tailed deer
Quercus rubra
Thuja occidentalis

ABSTRACT

Local, short- to medium-term studies make clear that white-tailed deer can greatly suppress tree growth and survival in palatable tree species. To assess how deer have broadly affected patterns of tree recruitment across northern Wisconsin, we analyzed recruitment success in 11 common trees species that vary in palatability across 13,105 USFS - FIA plots sampled between 1983 and 2013. We also examined how recruitment in these species covaried with estimated deer densities here. Saplings of five palatable species were scarce relative to less palatable species and showed highly skewed distributions. Scarcity and skew provide reliable signals of deer impacts even when deer have severely reduced recruitment and/or no reliable deer density data are available. Deer densities ranged from 2.3 to 23 deer per km^2 over a 30 year period. Sapling numbers in two maples (*Acer*) and aspen (*Populus*) with intermediate palatability declined sharply in apparent response to higher deer density. Path analysis also reveals that deer act to cumulatively depress sapling recruitment in these species over successive decades. Together, these approaches show that deer have strongly depressed sapling recruitment in all taxa except *Abies* and *Picea*. As these impacts are now propagating into larger sized trees, deer are also altering canopy composition and dynamics. The tools developed here provide efficient and reliable indicators for monitoring deer impacts on forest tree recruitment using consistent data collected by public agencies.

1. Introduction

In the United States, forest products generate over $200 billion a year in sales nationwide (USDA Forest Service, 2014). To maintain recreational and commercial use of these forests, managers must sustain forest growth by ensuring the responsible harvest of forest products and successful tree regeneration. Foresters often adjust management practices to enhance natural regeneration of desired species. Nevertheless, several ecological factors may act to inhibit seedling establishment, growth, and sapling recruitment. These factors include the often intense competition of seedlings and saplings for water, soil nutrients, and light (Aarssen and Epp, 1990; Dalling et al., 2011). Thus, species traits like drought and shade tolerance strongly affect a tree's ability to persist and compete for these resources. Seeds, seedlings, and saplings are also vulnerable to seed predation and a broad spectrum of herbivores including insects, birds, and mammals (Kolb et al., 2007). For some species like *Betula alleghaniensis*, a valuable timber species, the proportion of seeds that survive and persist into the sapling size classes is so low that these filters now serve to limit sapling recruitment and population persistence (Lorenzetti et al., 2008).

White-tailed deer (*Odocoileus virginianus*) now act as a key herbivore across much of northeastern North America limiting regeneration in many tree species (Rooney and Waller, 2003; Côté et al., 2004). Deer consume seeds, seedlings, and the buds, flowers, leaves, and sometimes bark and branches of saplings in palatable woody species exerting strong impacts in winter and early spring. They prefer to graze on graminoids and palatable understory forbs in spring through summer (Healy, 1971; Stormer and Bauer, 1980; Berteaux et al., 1998). Even when deer do not consume whole plants, their consumption of nutrient rich flowers, terminal meristems, and photosynthetic tissues tends to curtail growth and reproduction. Collectively and cumulatively, deer consume considerable understory biomass, strongly affecting energy and nutrient pathways. Ungulates also tread on plants and paw at leaf litter, destroying some plants and exposing mineral soil (Hobbs, 1996; Persson et al., 2000; Russell et al., 2001). Deer can also act as seed predators and sometimes as vectors to disperse seeds (Ostfeld et al., 1996; Gill and Beardall, 2001).

Through the latter 20th century, populations of white-tailed deer increased across much of the Eastern and Midwestern United States. In Wisconsin, populations have increased several fold since

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http://dx.doi.org/10.1016/j.foreco.2016.05.019
0378-1127/

the 1950s. Deer populations here now chronically exceed population goals in most Deer Management Units (WI DNR, 2015). Ecologists in the Upper Midwest (USA) first drew attention to the threats high deer populations pose to tree regeneration and forest plant communities in the 1940s and 1950s (Leopold et al., 1947; Dahlberg and Guettinger, 1956). Later ecological studies confirmed the reality of these threats by demonstrating shifts in the abundance, height, and demographic profiles of species sensitive to deer herbivory (Anderson and Loucks, 1979; Bratton, 1979; Marquis, 1981). In the Upper Midwest, the density and growth of several slow-growing, palatable woody species like *Tsuga canadensis*, *B. alleghaniensis*, and *Thuja occidentalis* have declined sharply in regions with abundant deer (Rooney and Waller, 2003; Rooney, 2001; Waller and Alverson, 1997). Understory forbs like *Trillium grandiflorum*, *Clintonia borealis*, and *Maianthemum canadense* also show strong declines where deer are abundant (Balgooyen and Waller, 1995; Frerker et al., 2014).

Because trees take many years to mature, declines in long-lived trees often occur long after deer herbivory occurs. This means we may not witness its full impact for decades (McGarvey et al., 2013). Forests subjected to prolonged, elevated deer densities continue to reflect these impacts for 20–70 years after release from deer browse pressure (Nuttle et al., 2014; Anderson and Katz, 1993; Balgooyen and Waller, 1995). In addition, these shifts in plant community structure and composition also strongly affect the abundance of birds, small mammals, and other components of diversity (Allombert et al., 2005; Cardinal et al., 2012; deCalesta, 1994; Fuller, 2001; Martin et al., 2012; McShea and Rappole, 2000; Ostfeld et al., 1996). These long-lasting impacts of deer herbivory could limit our ability to maintain and restore tree, understory plant, and animal diversity within North American forests. Such diversity supports significant ecological and economic values including populations of other wildlife species, an array of ecosystem services, recreational utility, and the timber value of commercially valuable hardwood species.

Ecologists use several methods to study deer impacts. These include tracking differences in growth rates, reproductive condition, the relative abundance of species, long-term shifts in community composition, natural experiments (Diamond, 1983, e.g., islands with and without deer), and manipulative experiments (e.g., fenced exclosures) (Côté et al., 2004; Waller, 2013). Although such studies provide valuable data, they are typically of short duration and apply primarily to the particular species that were studied and the local areas where the work was done. Exclosure studies that rigorously demonstrate strong deer effects on local plant communities are also sometimes criticized for making an extreme comparison between ambient deer effects and no deer at all. In addition, building and maintaining many exclosures over many years is expensive, often forcing us to rely on data from just a few exclosures at particular locations, reducing the generality of what we can infer. These concerns suggest that it would be useful to assess impacts of deer on tree regeneration across larger areas and a more natural range of variation in deer abundance. It would also be ideal if we could study deer impacts across multiple forest types, ages, and longer time periods, e.g., by linking local exclosure studies to longer-term regional trends (Frerker et al., 2014).

Here, we investigate regional variation in sapling abundance (recruitment) in 11 tree species in relation to variation in deer density that occurred over a 30 year interval and across all of northern Wisconsin. The broad scope of this study complements more intensive local short-term studies by providing a big picture of how deer are affecting tree recruitment in this region. To obtain this picture, we use systematic surveys of forest conditions pursued by the U.S. Forest Service in their Forest Inventory and Analysis (FIA DataMart, 2015) program (http://www.fia.fs.fed.us/). The FIA program surveys permanent plots arrayed on a regular grid at regular intervals (about 5-years). The number and dispersion of these plots (covering all forest lands in the U.S. since 1999) provide data of high statistical power from an unbiased set of samples. This allows us here to systematically compare variation in sapling recruitment among the chosen taxa in our region. In particular, we assess recruitment in 11 common tree species chosen to include taxa that differ in their palatability. These range from species that deer avoid (*Picea*) to species known to be highly palatable and susceptible to deer browsing impacts (*T. occidentalis* and *T. canadensis*). We hypothesized that saplings of species that are more palatable and susceptible to deer would be: (a) generally scarcer across the landscape, (b) absent altogether from many sites, and (c) scarcer at sites and in decades where they encountered higher deer densities. The deer density estimates we use for (c) also derive from a public source, namely the Wisconsin Department of Natural Resources (Wis-DNR). Because the metrics and approaches we describe use only publicly available data systematically collected by professional agencies, they do not require forest or wildlife managers to acquire new data or conduct local research.

Many local factors also affect patterns of tree recruitment including local soil and light conditions, local canopy composition and seed inputs, local deer browse preferences, and tree harvest history. We lacked consistent data for these and also note that obtaining such data would be impractical for most managers. In addition, our goal here was to analyze variation in recruitment at the coarser spatial scale of whole DMUs in order to obtain reliable aggregated signals of deer impacts for making management decisions. Our coarser scale of analysis ensures such averaging by filtering out much of the "noise" generated by the many variable local factors also affecting tree recruitment and deer-tree interactions.

2. Methods

2.1. Study region and estimates of deer density

Our study region encompasses the northern third of Wisconsin dominated by mixed hardwood forestlands (Fig. 1) providing a relatively homogenous set of landscapes for testing how deer affect tree recruitment. By limiting our study to this state, we could also use a single consistent set of deer density estimates from the Wis-DNR. They estimate annual post-hunt deer density using a Sex-Age-Kill (SAK) model in each of the 48 Deer Management Units (DMU) located in northern Wisconsin. Implementation of this model by the Wis-DNR provides relatively robust and reliable estimates of overwintering deer density with defined and limited amounts of error and bias (Millspaugh et al., 2009; VanDeelen, pers. commun.). Comparing SAK estimates with more rigorous Statistical Age-at-Harvest estimates that explicitly incorporate changing age structure and harvest rates indicates that the SAK model, as implemented in Wisconsin during our study period, tracked SAH estimates very closely in the northern forested DMUs (Norton et al., 2013). In addition, we only use the deer data in a comparative context to assess how variation in estimated deer numbers over DMUs and decades affects patterns of sapling recruitment in the chosen tree species.

The FIA plots occur at a density of about 1 plot per 1500 ha. We spatially divided these FIA plots into groups according to DMUs. The boundaries of these DMUs remained stable during the period of this study except for two large DMUs that were each split into two smaller units and one small DMU that was merged into a neighboring unit. For these, we recalculated estimated deer densities to match the new DMU areas. Our approach to hypothesis (c) assumes that enough variation exits in deer density among the DMUs and study periods to alter the abundances of small saplings.

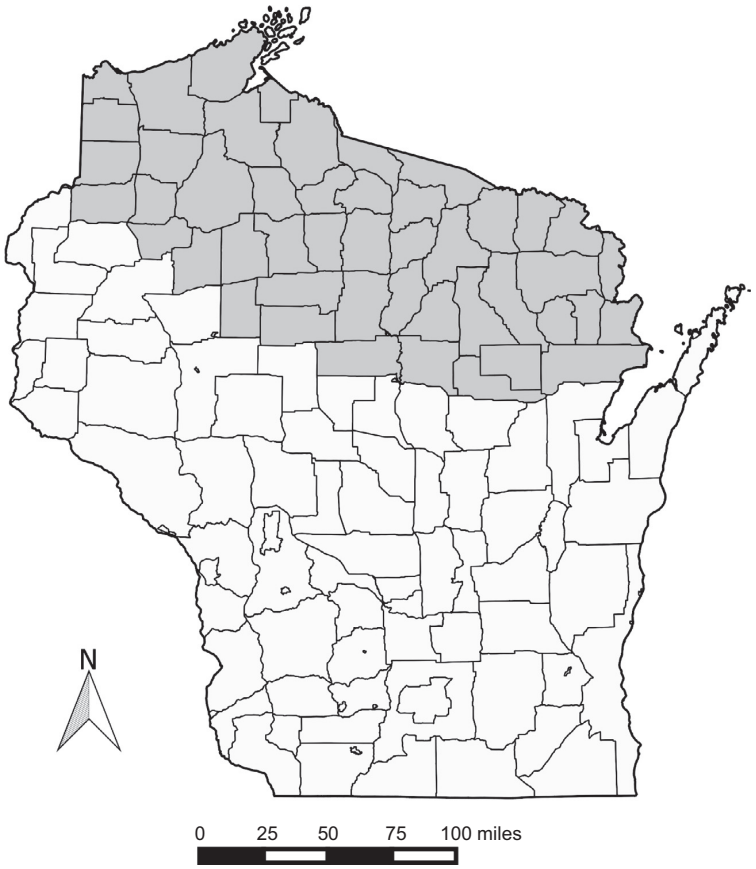

Fig. 1. Study area (shaded) in northern mixed hardwood region of Wisconsin. Note that this area does not include the Apostle Islands.

Levels of variation in estimated deer density over these DMUs and the 30-year period are ample (Fig. 2), justifying the "natural experiment" approach we use here.

Studies typically assess the number or height of tree seedlings or the incidence of deer browsing on seedlings and saplings within the "molar zone" (generally taken to be 0–180 cm above the ground). Such methods directly measure the immediate effects of browsing on local populations. Here, we sought instead to assess the cumulative impacts of prior deer browsing by instead tallying the number of small saplings (>2.54 cm DBH). The Phase 2 FIA data that we used ignores smaller saplings, making these the smallest trees for which we could obtain data. Trees >2.5 cm DBH are well established, 3–5 m tall, and have most of their foliage above the point where deer browse occurs (Kelty and Nyland, 1981), making them far less vulnerable to deer impacts. These thresholds are often used in deer browse studies (White, 2012; McGarvey et al., 2013; Bressette et al., 2012).

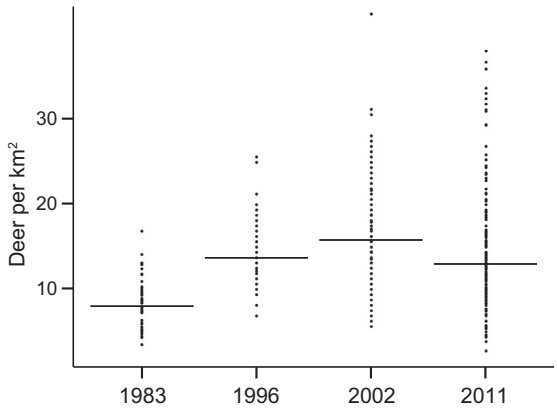

Fig. 2. Variation in estimated deer densities (deer per km^2) among Deer Management Units (DMUs) from 1983 to 2011. Note the high level of variation in estimated deer densities across DMUs and periods.

Because the number of FIA sampled saplings in a plot reflects a history of past browsing rather than current levels of browsing on smaller individuals in that stand, we analyzed variation in sapling recruitment in relation to estimates of deer density during the previous survey period (~10 years before the FIA sample year). The actual interval between when deer browsing occurs and the following FIA survey could be longer or shorter than this (likely longer in slow-growing species and perhaps shorter in fast-growing species). Given the decadal sampling regime and the broad scale of these surveys, we deemed 10 years to be the appropriate interval for evaluating deer effects. Analyses based on other lags showed weaker relationships to estimated deer density.

2.2. Study species and palatability

We focused on 11 common tree species known from previous studies to vary in their palatability to deer and sensitivity to browsing (Table 1). We specifically included two unpalatable

Table 1
Assigned browse sensitivity classes for the 11 focal taxa. Class 1 includes the least palatable species and Class 4 those that are most palatable and vulnerable to deer. Note the far higher skew values (bolded) in the abundance distributions of the (log) number of small saplings in the more palatable taxa relative to less palatable taxa or larger trees of the same species.

Scientific name	Common name	Palatability class	Skew in log (# of small saplings +1)	Skew in log (# of large trees +1)
Abies balsamea	Balsam fir	1	0.02	0.0283
Picea spp.	Spruce	1	0.60	−0.1476
Acer rubrum	Red maple	2	0.82	−0.501
Acer saccharum	Sugar maple	2	0.02	−0.41
Populus tremuloides	Quaking aspen	2	0.04	0.3181
Pinus strobus	White pine	3	**2.18**	−0.2047
Quercus rubra	Northern red oak	3	**1.66**	0.1289
Betula alleghaniensis	Yellow birch	4	**1.47**	−0.16253
Thuja occidentalis	Northern white cedar	4	**2.52**	−0.1387
Tsuga canadensis	Eastern hemlock	4	**2.00**	0.25734

genera (*Picea* and *Abies*) in order to provide a control that would allow us to detect any general spatial or temporal trend in tree recruitment unrelated to deer herbivory. We assigned the taxa to one of four palatability classes *a priori* based on published preference results for our region (e.g., Dahlberg and Guettinger, 1956), a local exclosure study (Frerker et al., 2014), and our own expert opinion (based on 25 years of field work on deer impacts in Wisconsin and wide reading of the relevant literature). As *Picea glauca* and *Picea mariana* are similarly distasteful to deer and difficult to distinguish, we combined these into the genus *Picea*.

2.3. Assessing variation in tree recruitment

To obtain data on the abundance and sizes of trees for these ten taxa, we accessed the USDA National Forest Service Forest Inventory Analysis (FIA) "DataMart" via www.fia.fs.fed.us/tools-data. The FIA program resurveys long-term forest plots nation-wide. In Wisconsin, these commenced with intensive periodic surveys in 1983 and 1996 (roughly 1 plot per 1000–1500 ha). They then transitioned to less-intensive (roughly 1 plot per 7000 ha) annual surveys in 2000. We use tree data from 13,105 FIA plots in our region spanning the period 1983–2013 divided into four periods. To account for differences in sampling intensity across inventories, surveys from 2000 to 2004 and 2009–2013 were aggregated together to create similar plot densities (without duplication as plots are resurveyed on a 5-year cycle). We refer to these aggregations as inventory year '2002' and '2011', respectively. We divide trees in the FIA surveys into three size classes: small (2.54–5.08 cm DBH), medium (5.08–10.16 cm DBH), and large (>10.16 cm DBH).

2.4. Statistical analyses

To address hypotheses (a) and (b), we first tallied numbers of saplings and trees in each of the three size classes within each DMU and decade by species and palatability class. We averaged values across all plots within each DMU and period. Because these values varied widely and included many zeros, we add one to all values and log transform the averages. This homogenized the residual error variances among taxa and treatments, meeting assumptions of our linear models and facilitating comparisons among species, palatability classes, DMUs, and periods where abundance counts differed greatly. These transformed numbers of small saplings provide a primary indicator for tree regeneration. On this scale, values of 0 reflect sites with no saplings: $\log(0+1)$. This was the mode for the more palatable species. We assess demographic inertia between the numbers of small and medium saplings using simple correlations between these transformed values. We also compare the abundance of saplings and larger trees among the palatability classes and decades. This allowed us to evaluate whether saplings numbers in more palatable classes varied independently of tree numbers, as expected if deer control their numbers. We also compare patterns of recruitment among the palatability classes to see whether recruitment in the palatable taxa differs from recruitment in unpalatable *Picea* and *Abies*. We plot and evaluate the distributions of sapling numbers in each species to see whether these differed in shape in a diagnostic way between more and less palatable species (hypothesis (b)). Note the use of two controls here: the numbers of adult trees in the same taxon and sapling numbers in the unpalatable taxa.

To address question (c), we compare the extent to which variation in sapling abundance within palatability classes and species covaries with estimated deer densities within that DMU in the preceding time period. In more browse-sensitive species, we expect the proportion of small saplings to decline in DMUs and decades experiencing higher deer densities but little to no effect of deer density in taxa that deer avoid. Here, we use two complementary approaches. The first used general linear models to evaluate the effects of palatability class and decade on the abundances of small, medium, and large size class trees (questions a and b). This approach implicitly assumes independence in these tree numbers among the DMUs and across the three successive decades of the FIA data. To address the latter assumption, our second approach modeled autocorrelation explicitly using path analysis (see below). We plotted the adjusted means and error bars from the first analysis to compare levels of recruitment among the palatability classes and decades and overall changes in the abundances of small, medium, and larger trees. If deer reduced the densities of saplings in more palatable species, we expect a strong main effect of palatability class on the abundance of small saplings. With regional changes in deer density or another broadly acting ecological factor, we also expect a main effect of decade. Finally, if numbers of small saplings (henceforth "saplings") in more palatable taxa decline more in decades with more deer, we expect a significant decade by palatability class interaction.

We also tested for deer effects more directly by analyzing variation in small sapling recruitment in relation to both palatability class and previous deer density using DMU estimates from the previous decade as a covariate. Here, again, we expected saplings of more palatable species to be scarcer and for deer abundance to affect sapling abundance more in palatable than in less palatable species (tested using the palatability class $\times$ deer interaction term). We also analyzed models for individual species. Because species' responses to deer varied greatly (deer density $\times$ species interaction term $F = 8.11$, $p < 0.001$), we analyzed separate models for each taxon. We modeled sapling recruitment as a function of deer density and deer density squared (to account for non-linear effects. We then sequentially dropped non-significant effects in each model to obtain a final model for each species, always retaining the deer effect.

Our final approach analyzed deer effects using path analysis to model tree recruitment in successive decades as a function of sapling numbers and estimated deer densities in the preceding decade (Fig. 7). Path analysis assumes that variables can be placed into causal order, as is the case here given the sequence of events and known effects of herbivory on plants. It also assumes that the modeled predictor variables have linear and additive effects on the dependent variable, assumptions we tested before applying the model. In particular, we summed the (log) number of saplings in palatability class 2 (*Acer rubrum*, *Acer saccharum*, and *Populus tremuloides*) within each decade and DMU and modeled these abundance values as a function of estimated deer densities and sapling numbers in the preceding decade. We applied the model to this palatability class because these species produce abundant seeds and seedlings that provide good indicators for evaluating deer impacts in our region (see below). The path analysis explicitly addresses sequential causal dependencies and the autocorrelation present in these data. We used both R (RStudio: Integrated Development for R, Boston, MA) and JMP (vers 11.2.1) for these analyses (SAS Institute, Cary, NC).

3. Results

3.1. Variation in deer densities and sapling abundances

Deer densities varied widely across the region and over time, providing the variance necessary to infer deer effects on sapling numbers (Fig. 2). We also observed substantial variation among sapling numbers across sites within species (Fig. 3). However, these distributions differed in shape among species and palatability groups. The five taxa in palatability classes 1 and 2 showed positive modes and approximately log-Normal distributions (e.g., *A. rubrum*, Fig. 3a). In contrast, the five species in palatability classes 3 and 4 all showed modes of 0 (reflecting no saplings within the plot) and highly skewed distributions relative to both the less palatable species (Fig. 3b) and to adult trees in the same species. The five more palatable species showed far more skewed distributions of (log) sapling numbers than the less palatable species (means: 1.97 vs. 0.3, Table 1). Sapling numbers were also far more skewed in palatable species relative to adult trees in the same species (mean difference 0.44 in the five less palatable species vs. 1.99 in the more palatable species, paired *t*-test: $t = 3.94$, $p = 0.003$). The presence of adult trees at most sites that lacked palatable saplings suggests that site suitability is not limiting recruitment in these species. We conclude that a syndrome involving very low mean sapling abundance, a mode of 0, and a highly skewed distribution provides a plain and useful signal for inferring strong deer impacts. Surprisingly, this signal emerged for half the taxa studied here. Skew was also noted in seedling counts of some tropical trees and used to predict subsequent demographic dynamics (Feeley et al., 2007).

3.2. Palatability classes compared

The abundance of small saplings differed greatly among the four palatability classes and across the four decades (Fig. 4; Table 2). Taxa known to be sensitive to browsing (palatability classes 3 and 4) have far fewer small saplings than taxa that tolerate or repel browsing (classes 1 and 2). The abundances of medium-sized saplings parallel those of the small saplings across decades and the palatability classes (top and middle rows of Fig. 4) where palatability class has a similarly large effect ($F = 78.2$ vs. 66.4, Table 2). We confirmed demographic inertia between size categories using correlations within each species which ranged from +0.51 in *Quercus* to +0.85 in *Abies* (all $p < 0.001$). In contrast, the abundance of larger trees only loosely reflects palatability. The more palatable classes 3 and 4 had many more adults than juveniles (Fig. 4; Table 2). Thus, the scarcity of saplings in these species does not reflect a lack of seed inputs.

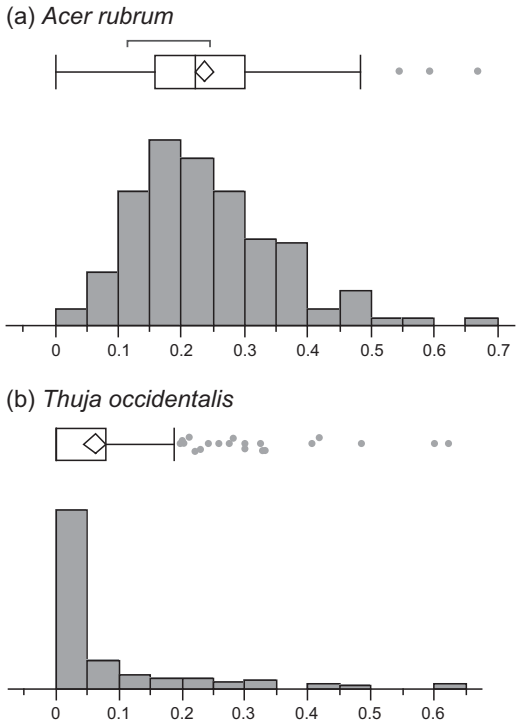

Fig. 3. Distributions of red maple and northern white cedar sapling numbers among stands. Frequency histograms show the logarithm of the mean number of small saplings (+1) in all stands. Note the approximately log-Normal distribution of sapling abundances in red maple (a), a prolific seeder of intermediate palatability to deer, and the highly skewed distribution in cedar (b) which is highly palatable and susceptible to deer browse. Mean, variance, skew, and sample sizes for red maple: 0.236, 0.012, 0.816, N = 192, and cedar: 0.064, 0.013, 2.52, N = 163.

Across decades, numbers of small saplings increased between 1983 and 1996 and then declined (Fig. 4). This may reflect an initial period of improving regeneration followed by declines in regeneration as increased deer populations (Fig. 2) curtailed regeneration. This apparent lag supports using previous decade deer densities to infer deer effects. Remarkably, these two simple predictors, palatability class and decade, together account for half of the observed variation in sapling abundance (Table 2).

In the models that explicitly include estimated deer density (at the whole DMU level) as a predictor, deer have a strong negative main effect ($F = 75.8$, $p < 0.001$) but their effect also varies significantly among the palatability classes (deer × palatability interaction $F = 12.5$, $p < 0.001$, Table 3; Fig. 5). Analyses of individual interaction terms show that dramatic declines in sapling numbers as deer increase in palatability class 2 account for most of this effect (Table 3). We expected the relation between sapling numbers and deer density to disappear in unpalatable species but were surprised to also see little response to deer in palatability classes 3 and 4. Again, a model that includes only the effects of DMU average estimated deer density and palatability class accounts for a large proportion (39%) of the total variation observed across sites and decades in small sapling numbers (Table 3). Models with more local estimates of deer abundance would likely do even better.

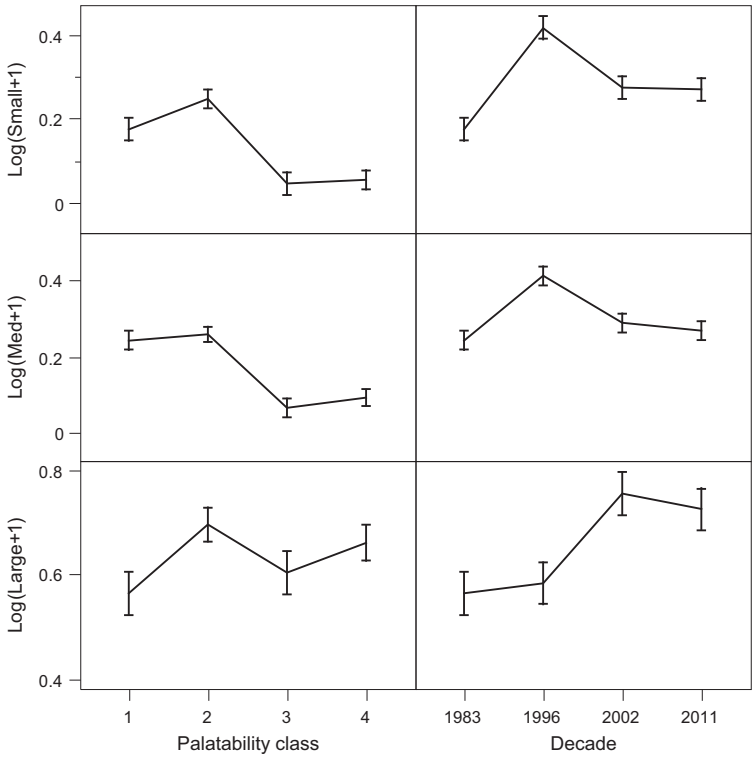

Fig. 4. Variation in the numbers of saplings and trees among palatability classes and decades. Values reflect the (log) mean number of trees per stand in all three size classes (small saplings 2.5–5.1 cm DBH, medium saplings 5.1–10.2 cm DBH, and large sapling >10.2 cm DBH). Values are adjusted means correcting for DMU and decade. Error bars show ± one S.E. Note different scale for the number of large trees.

Table 2
Variation in tree abundance among palatability classes. The table shows results from analyses of variance of the logarithm of the number of small, medium, and large sized trees (+1) analyzed over the four palatability classes (1 = least, 4 = most palatable) and decade. The values shown are F-ratios. All values shown are significant at $p < 0.001$. Adjusted means from these analyses appear in Fig. 3.

Factor	DF	F-ratios		
		Small	Medium	Large
Palatability	3	66.38	78.16	9.81
Decade	3	52.19	16.86	22.52
Decade * palatability	9	10.86	7.77	6.26
Overall r^2 values		0.503	0.484	0.21

3.3. Species-specific responses

Analyses of individual taxa confirm that species of intermediate palatability show the greatest sensitivity to estimated deer density (Table 4, Fig. 6). Deer effects in *Picea* and *Abies* are negligible, confirming that they serve well as controls. Sapling numbers in five species (mostly in palatability class 2) decline in apparent response to increasing deer density. Sapling recruitment in *A. rubrum* and *saccharum* and *P. tremuloides* all declined greatly as deer became more abundant, accounting for the sensitive response to deer in palatability class 2 (Fig. 5). Sapling numbers in red oak (*Quercus rubra*) and yellow birch (*B. alleghaniensis*) were lower but also declined conspicuously in areas/times of higher deer density. Although we classed balsam fir (*Abies balsamea*) as unpalatable, it showed an almost significant decline in abundance in response to deer (Table 4). We were initially surprised to find no apparent response to deer in *T. canadensis* and *T. occidentalis*, two slow-growing conifers known to be highly susceptible to deer browsing (Table 4, Fig. 6). We also found an apparent positive effect of deer on sapling numbers in *Pinus strobus*. These effects, however, were small reflecting the absence of saplings at most sites in these species and corresponding low power for detecting any deer signal. Regeneration was so restricted in these species that intercepts of their fitted regressions (the numbers of small saplings expected when deer are absent) did not differ significantly from zero.

3.4. Path analysis

The path analysis (Fig. 7) allowed us to explicitly model sequential time dependencies and the autocorrelation present in our data sets. Deer densities in each decade strongly affected deer densities in the following decade (beta values: 0.64–0.75), as did sequential sapling abundances in palatability class 2 (beta = 0.43–0.46, Table 5). The direct effects of deer were always appreciable and negative with beta values of −0.27 to −0.42. Interestingly, all the 2- and 3-step indirect effects were also negative and of the same magnitude (betas from −0.32 to −0.43). Thus, over successive decades, as the model includes more information about deer densities and sapling numbers in preceding decades, the indirect effects of deer accumulate to become much larger than the direct effects (Table 5). This strongly implies that the effects of deer analyzed in the preceding GLM models substantially underestimate the actual total effects of deer on tree regeneration in these forests.

Table 3
Recruitment variation over palatability classes in relation to deer. The table shows results from the general linear model analyzing variation in the (log) number of small saplings in relation to assigned palatability class, estimated deer density during the previous study period, and their interaction. Note that although all four palatability classes differ strongly in small sapling abundance, only class 2 species show significant declines in saplings with increases in estimated deer density. Overall F = 123.3 (df = 7, 1343).

	Df	Sum Sq	Mean Sq	F value	Pr(>F)	
Palatability	3	429.24	143.081	249.897	<2.20E−16	***
Deer density	1	43.38	43.375	75.757	<2.20E−16	***
Deer density:palatability	3	21.42	7.141	12.472	4.79E−08	***
Residuals	1343	768.95	0.573			

Dependent variable: log(small + 1)

	Estimate	Std. error	t value	Pr(>|t|)	
(Intercept)	0.450	0.032	14.124	<2.00E−16	***
Palatability2	0.134	0.039	3.466	0.000546	***
Palatability3	−0.291	0.053	−5.507	4.36E−08	***
Palatability4	−0.353	0.051	−6.977	4.71E−12	***
Deer density	−0.003	0.001	−2.140	0.032572	*
Deer density:palatability2	−0.007	0.002	−4.071	4.95E−05	***
Deer density:palatability3	0.001	0.002	0.580	0.561692	
Deer density:palatability4	0.003	0.002	1.166	0.244006	
Observations	1350				
R^2	0.391	Adj R^2	0.388		

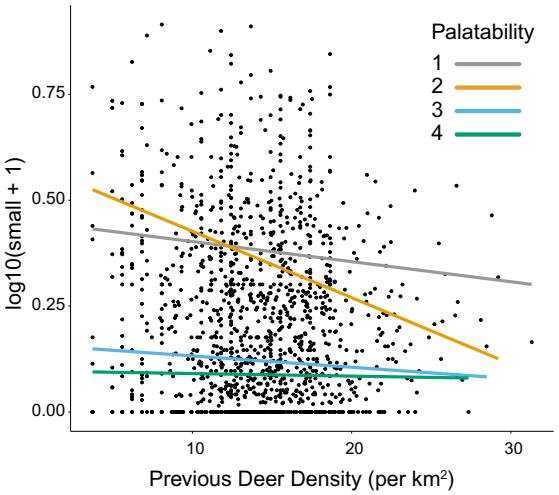

Fig. 5. Deer effects on the number of small saplings by palatability class. Deer density estimates are for each DMU in the previous sampling period (about 10 years earlier). Based on the model of sapling numbers in Table 3. The scarcity of small saplings in Palatability classes 3 and 4 precluded significant deer density effects there but class 2 shows a highly significant decline in sapling numbers in relation to deer density ($p < 0.001$).

Table 4
Deer affect sapling recruitment within species. These results derive from the separate models fit to the number of small saplings (log of (number +1)) for each species (totals within each DMU and time period). Species are listed in order of their palatability classes (Table 1, with classes 1 and 3 marked on left). "Deer β" refers to standardized partial regression coefficients for the linear effects of Wisconsin DNR estimates of deer density within each Deer Management Unit (DMU) during the previous time period (roughly 10 years earlier). Labels show levels of significance: $^{***}p < 0.001$, $^{**}p < 0.01$, and $^{*}p < 0.05$, AS $p < 0.10$. The influence of quadratic (Deer^2 β) terms are also shown and included in the model when these were significant. Average stand basal area (weighted by each species' abundance across stands within each DMU) was also included in the model when it was significant (in *Picea*, *Populus*, and *Tsuga*, resulting in beta values of −0.279, −0.14, and 0.471, respectively). The r^2 terms show overall coefficients of determination for each model. Intercept values show the densities of saplings expected at a deer density (and basal area) of 0 given the model. Values that do not differ significantly from 0 are **bolded**.

Species	Intercept	Deer β		Deer^2	β	r^2
Picea spp.	0.463	−0.002				0.08
Abies balsamea	0.500	−0.158	AS			0.02
Acer rubrum	0.405	−0.342	***	0.17	*	0.14
Acer saccharum	0.507	−0.379	***			0.14
Populus tremuloides	0.952	−0.435	***			0.19
Pinus strobus	**0.042**	0.119	*	0.179	*	0.03
Quercus rubra	0.249	−0.229	*			0.03
Betula alleghaniensis	0.165	−0.309	**			0.10
Tsuga canadensis	**0.012**	0.045		0.241	**	0.17
Thuja occidentalis	**−0.018**	0.168		0.276	**	0.09

4. Discussion

The metrics and methods applied in this study all point to the conclusion that browsing by white-tailed deer strongly limits patterns of tree recruitment in the forests of northern Wisconsin. Deer have considerably reduced regeneration in many tree species of intermediate palatability and eliminated it altogether at most sites in several conifer species known to be sensitive to deer browsing. This is highly relevant for deer management in that stands of these conifers provide key habitats for overwintering deer. These stands will likely disappear given this regional failure in regeneration. These effects are not local, temporary, or restricted to a few sensitive species. Rather, they extend across all of northern Wisconsin, cover a 30 year period, and affect most (8 of 10) of the tree species examined. These effects have also begun to modify the composition and structure of the mid-stories of these forests. It will not be simple to limit or reverse these impacts, but without these data and analyses, we could not assess the full scale and extent of the impacts deer are having.

The results of this study plainly indicate that we must use different indicators to detect and monitor deer impacts on forest tree regeneration in different species in this region. Current and previous levels of deer browsing were so heavy in the five most palatable species that small saplings were scarce to absent at most sites. Sapling densities were too low in the highly palatable conifers to accurately measure regeneration or to relate variation in regeneration to deer density. For these species, the absence of small saplings is itself the best indicator, as quantified by very low means, modes of zero, and highly skewed distributions of sapling numbers. Fortunately, these indicators are easily extracted from the FIA data and can be used even when data on deer densities are suspect or lacking.

Species of lower palatability to deer had more abundant saplings allowing us to examine how mean sapling abundance varied

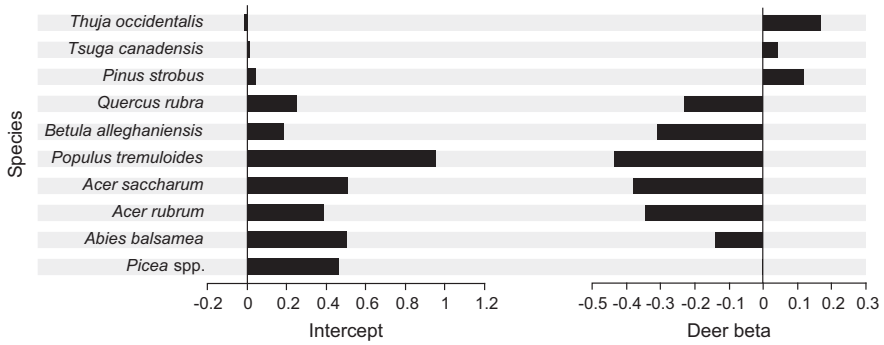

Fig. 6. Variation among species in sapling abundance and apparent deer effects. Species appear in order of their predicted palatability to deer from highly palatable conifers (top) to least palatable taxa (*Picea* and *Abies*) at the bottom. The left side shows intercepts from the models fitting (log) small sapling abundance to regional variation in estimated deer densities (from Table 4). Intercepts close to zero (top) reflect species with very few small saplings even at relatively low deer densities. The right side shows the estimated effect of deer (β values) on variation in small sapling numbers by species. Direct deer effects are most easily detected in abundant species of intermediate palatability.

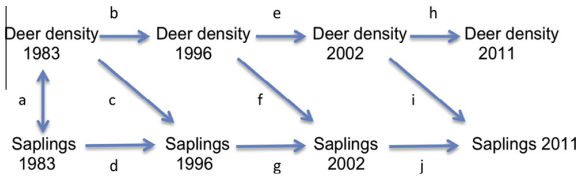

Fig. 7. Path diagram showing effects of deer on patterns of sapling recruitment. Tree data reflect sums of the average number of small saplings in palatability class 2 (*Acer rubrum*, *A. saccharum*, and *Populus tremuloides*) across all stands within a particular DMU and decade. Deer densities are Wisc DNR estimates for each DMU and decade. Path coefficients for each lettered path appear in Table 5.

with respect to estimated deer density. In these species, we found highly significant negative associations, strongly supporting hypothesis (c) and providing an altogether different method for inferring deer impacts. Having these two independent indicators that apply to separate but overlapping sets of species that differ in regeneration success adds range and flexibility to the tools that forest and wildlife managers can use to monitor and assess deer impacts. Together, these metrics support all three hypotheses (a), (b), and (c) that saplings of highly deer-palatable species are now scarce to absent across much of our region and that deer densities strongly affect sapling abundance in several species of lower palatability.

Research in the eastern and Midwestern U.S. has already shown that *T. occidentalis*, *T. canadensis*, and *Q. rubra* are highly palatable to deer and have failed to regenerate in many forests (Strole and Anderson, 1992; Boerner and Brinkman, 1996; Waller et al., 1996; Alverson and Waller, 1997; Rooney et al., 2000, 2002; Collins and Carson, 2002). All these studies identify white-tailed deer as the key factor limiting the density or size of seedlings or saplings in these species. The limitation of these studies has only been that they have focused on regeneration at a limited number of sites and documented these failures over limited periods of time. These limitations have allowed some to argue that these failures are local, temporary, and/or only apply to a few highly palatable species. In contrast, our study exploited the vast amount of information contained in the FIA database to show that deer have curtailed sapling recruitment in most of the tree species studied and have had these strong impacts over at least 30 years and a huge region reflecting a diversity of forest types, ownerships, and methods of management. Our results thus complement and amplify results from more local studies by confirming that the common evidence of local regeneration failure they have documented apply much more broadly to multiple species, most sites, and an extended period of time.

Numbers of tree saplings varied strongly among the palatability classes. As predicted, we found many fewer saplings in classes 3 and 4 than in 1 and 2. Decade and palatability class alone account for more than half (51%) of the total variation in regeneration success observed across all tree species studied and all 13,105 sites. For such simple predictors to provide such high explanatory power is rare in complex ecological systems occupying a diverse and heterogeneous region. Substituting estimated deer densities for

Table 5
Results from the path analysis model of recruitment in palatability class 2 (*Acer rubrum* and *saccharum* and *Populus tremuloides*). "Path" refers to the paths labels in Fig. 7 that connect particular predictor and dependent variables. Beta values are the path coefficients (standardized partial regression coefficients). Significance labels for individual predictors as in Table 4. The direct effects of deer on (log) sapling numbers in successive decades are shown in the "Direct effect" column. Indirect effects on bolded sapling numbers reflect the delayed effects of deer in an earlier decade as expressed through their effects on later deer abundance and sapling numbers. These involve products of the path coefficients (e.g., the b * f + c * g two-step indirect effects on saplings in 2002 and the e * i + f * j effects on 2011 saplings). Note that total deer effects increase steadily over time as these consistently negative indirect effects cumulatively affect the number of surviving saplings.

Path	Predictor	Dependent Var	Beta	Signif	Direct effect	Indirect (2 steps)	Indirect (3 steps)	Total deer effect
a	Deer 83	Saplings 83	0.096	NS				
b	Deer 83	Deer 96	0.639	***				
c	Deer 83	**Saplings 96**	−0.311	*	−0.311			−0.311
d	Saplings 83	Saplings 96	0.447	***				
e	Deer 96	Deer 02	0.748	***				
f	Deer 96	**Saplings 02**	−0.270	*	−0.27	−0.317		−0.587
g	Saplings 96	Saplings 02	0.465	***				
h	Deer 02	Deer 11	0.723	***				
i	Deer 02	**Saplings 11**	−0.417	**	−0.417	−0.429	−0.337	−1.183
j	Saplings 02	Saplings 11	0.434	**				

decade in these models still provided high explanatory power (39%) despite the fact that these DMU estimates reflect spatial averages that ignore all the local variation in deer densities and site conditions affecting tree regeneration within these DMU's (Wisconsin DNR, 2006). As judged by F values, palatability consistently emerged as the most important predictor of sapling abundance and one that always interacted strongly with the deer effect, exactly as predicted. The fact that statistical models that ignore all local variation in soil and light conditions known to greatly affect patterns of tree regeneration had such high explanatory power strongly suggests that deer browsing has emerged as the dominant force controlling patterns of tree sapling recruitment in these forests.

Saplings became progressively scarcer in the higher palatability classes (3 and 4) coincident with the emergence of conspicuous skewed sapling abundance. This high skew with a mode of 0 demonstrates that some factor acted at most sites to eliminate regeneration altogether. Saplings in browse-sensitive *B. alleghaniensis* and *Q, rubra* were still abundant enough to show strong deer effects (with betas of −0.31 and −0.23, respectively). Their sapling distributions, too, however, show high skew and an absence of saplings at many sites. Deer exclosures in our region confirm that yellow birch seedlings become scarce where deer are common (Frerker et al., 2014). If saplings in *Betula* and *Quercus* become even more scarce, it will become impossible to detect direct deer effects from among-site variation in sapling abundance.

We are the first to propose using a very low sapling abundance and high skew in (log) sapling numbers relative to adult trees of the same species as plain and simple signatures of deer impacts. We observed that diagnostic signature in half the species studied here, but only in species with higher palatability to deer. We further note that anyone with access to FIA data for their area can easily compute these metrics and that computing these to infer deer impacts requires no data whatsoever on estimated deer densities, local rates of browsing, local seedbed conditions, or any other labor-intensive field measurement. The mode of 0 saplings with very high skew together provide a useful and reliable signature of deer impacts with skew (of log sapling number) emerging as more diagnostic. Feeley et al. (2007) also identified skew as a useful metric as it correctly predicted the direction of population change within two Malaysian forests for ~75% of the species. They also found, however, that trends within one forest did not serve to predict demographic changes at the other site. We expect that the far broader sampling enabled by the FIA data should allow more accurate inferences regarding regional trends. This conjecture and the skew and mode metrics should, however, now be tested in other systems.

Trends in our two controls (adults of the same species and the unpalatable taxa) served well to confirm that the metrics we used to infer deer impacts provide robust and reliable signals. The abundances of larger trees were largely uncoupled from patterns of sapling recruitment, confirming that trees are there to provide seed inputs and that sites are indeed suitable for these species. Saplings of unpalatable taxa (*Picea* and *A. balsamea*) occurred commonly at most sites but their abundance did not covary with deer abundance. These controls support the conjecture that deer rather than some other factor has acted to limit tree recruitment in these forests. Surprisingly, deer may even have acted to depress *Abies* sapling abundance (beta = 0.16, p = 0.06). Deer generally only consume *Abies* when other browse is scarce (Dahlberg and Guettinger, 1956; Tremblay et al., 2005).

We exploited natural variation in deer density across our region as a "natural experiment" to explore how deer affect patterns of regeneration in our studied species. In our region, densities are lowest in the larger Ojibway and Menominee Indian reservations where densities usually remain less than 4 per km^2 (Wisc DNR data, R. Rolley). Deer densities clearly also vary greatly in response to local habitat conditions, current and recent hunting pressure, and levels of predation (Leopold, 1933). Despite this local variation in deer abundance and the imprecision inherent in the Wis-DNR SAK estimates of deer density, these whole DMU estimates of deer density worked surprisingly well to predict regional variation in the density of saplings in five of the ten taxa we studied (Table 4). These included two important sawtimber species (*Q. rubra* and *B. alleghaniensis* in palatability classes 3 and 4, respectively) as well *Acer* and *Populus* with intermediate palatability. The historical depth of the SAK deer estimates and abundance of these species also allowed us to demonstrate both immediate effects of deer on sapling numbers and how deer affected sapling recruitment over successive decades using path analysis. These cumulative impacts acted to multiply total deer impacts in these moderately palatable tree species over the 30 years of this study. Results from the path analysis also suggest that the recent deer effects examined in the simpler models actually underestimate total deer effects by ignoring how deer impacts accumulate over successive decades.

The species showing the strongest responses to deer abundance had intermediate palatability (class 2, *A. rubrum* and *saccharum* and *P. tremuloides*). These widespread trees often dominate sites where they occur. They produce prolific numbers of seeds and seedlings that then recruit to become the saplings counted in the FIA surveys. The high numbers of seedlings these species produce could help to swamp local herbivores like deer by improving survival odds for individual seedlings when many are present. Such effects could also cause sapling numbers to decline non-linearly as deer populations increase as many saplings could survive when deer are low relative to seedling numbers but few to none may survive when deer become more abundant. Such effects probably contribute to the high skew we observed in the more palatable species as well as the steep declines in sapling recruitment with deer density in *Acer* and *Populus*. The abundant seedlings and saplings in these species also give us a tool for tracking deer impacts even when deer are dense enough to eliminate regeneration in more palatable species.

Seedlings and saplings of *P. strobus*, *T. canadensis* and *T. occidentalis* are all highly vulnerable to deer that often browse preferentially on these conifers, particularly in winter (Dahlberg and Guettinger, 1956; Alverson and Waller, 1997; Rooney et al., 2000, 2002; Cornett et al., 2000; Townsend et al., 2002; Vila et al., 2003). Saplings of these species were so scarce across the region that no saplings occurred at most sites. Their scarcity prevented us from being able to detect any decline in sapling numbers as deer densities increased. We even observed weak positive relationships in two cases (though the intercepts in these cases were indistinguishable from zero). It would be useful in this context to do numerical simulations to reduce ("rarify") sapling data to see when clear negative relationships drop to the point of non-significance.

We did not examine the effects of management practices in this study but know that management can enhance seedling establishment in many of the palatable species, e.g., by providing substrates suitable for germination and early growth (Rooney et al., 2002; Curtis, 1959; Doepker and Ozoga, 1990). Improving seedling establishment, however, does little to improve recruitment to size classes above 2 m in height in the shade-tolerant evergreens we studied as slow-growing seedlings must pass through a long period of vulnerability to deer before they escape the "molar zone" (Waller et al., 1996; Rooney and Waller, 1998; Rooney et al., 2000). Silvicultural treatments that enhance light conditions, however, might accelerate seedling growth enough to improve recruitment in some cases.

Accepting both the scarcity and skew of sapling numbers and negative effects in the linear models as signals of deer impacts,

we find strong evidence for these in eight of the ten taxa we studied. Populations of slow growing tree species take 70+ years to recover from prolonged browsing (Frelich and Lorimer, 1985; Anderson and Katz, 1993). Thus, deer impacts manifest now will persist for many decades to a century or more (McGarvey et al., 2013). Once saplings have failed to regenerate for several decades, the abundance of those species in the canopy will decline. This, in turn, will reduce the input of seeds, further depressing seedling recruitment. The slow rate of these processes delays both our ability to recognize that deer impacts are occurring and our ability to reverse such declines already underway. Thus, we should be vigilant in monitoring patterns of regeneration and addressing causes of regeneration failure if we intend to sustain the diversity and relative abundance of trees that in these forests and the commercial value they represent.

Tree regeneration across northern Wisconsin is now somewhat limited by deer browsing in three of the ten taxa examined, strongly limited in another two, and severely limited in three conifer species. Different signatures of deer browsing are evident in these species depending on seedling abundance, how susceptible their seedlings are to browsing and their rates of growth. These metrics should now be tested in other systems to confirm that FIA data can be put to similar use elsewhere. Because FIA data are already systematically collected for other purposes, using them to estimate deer impacts brings high power at low cost. We gain additional power when we also have access to reliable data on deer densities extending over several decades.

The absence of any routine widespread monitoring system has stymied our ability to reliably infer the extent and severity of deer impacts on forest ecosystems. State and federal agencies can now capitalize on the FIA data to routinely monitor deer impacts in a systematic and sustained way. Sharing these results widely with foresters, hunters, and the public could improve public understanding of deer threats and public support for professional management actions to address those threats. The results presented here strongly support the need to limit deer densities to promote healthy forest regeneration. As always, we should check assumptions, use controls, and accept the limitations involved in using FIA and DNR data. Foresters, forestland owners, and wildlife agency personnel may be keen to use these results to enhance efforts to control deer populations. Limited "band-aid" solutions to browsing such as fencing deer out or protecting individual seedlings are expensive and do not serve to protect other elements of plant and animal diversity sensitive to deer impacts. Once we better understand how forests and wildlife populations interact, we should be able to better manage both as an integrated and dynamic system.

Acknowledgements

We thank the U.S. Forest Service FIA program and particularly C. Barnett and E. LaPoint for their assistance in accessing and using the FIA data. R. Rolley of the WI DNR helped us to access and interpret the deer population data. T. Van Deelen helped us understand the utility and limitations of the SAK deer estimates. J. Ash and D. Li provided statistical advice. R. Toczydowski, A. Sabo, and G. Sonnier provided helpful comments on the manuscript. S. Friedrich redrew the figures. DMW is grateful for the favorable working conditions and sabbatical support provided by O. Ronce, I. Olivieri, the LABex program, and the ISEM group at the Université de Montpellier, France.

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