

Accuracy of Whitebark Pine and Limber Pine Identification by Forest Inventory and Analysis Field Crews

Shayla R Williams, James E Steed, Jeremy Morrone, Sara A Goeking, Matt Lavin, Erich Kyle Dodson, Rachel E Simons

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Forest Science

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Abstract:	Accurate identification of whitebark and limber pine has become increasingly important following the 2022 listing of whitebark pine as a threatened species under the Endangered Species Act. However, morphological similarities make identification of the two species difficult where ranges overlap. Using a genetic test that differentiates whitebark and limber pine, we compared field identification by Forest Inventory and Analysis field crews with genetic identification for needle samples from 371 trees. Field identifications were 100% correct for the 76 samples collected from outside regions of species' range overlap. Eighty-three percent of the field identifications were correct in regions of range overlap (89% for large trees, 88% for saplings, and 78% for seedlings). Field-identified samples were correct 60% of the time for limber pine and >99% for whitebark pine. Random forests analysis revealed that identification accuracy is influenced by crew experience, large (≥ 12.7cm diameter) limber or whitebark pines recorded by field crews on the plot, elevation, Julian day of sample collection, and habitat type. We found that whitebark pine has likely been underestimated, and limber pine overestimated, within their overlapping ranges. We provide insights on improving accuracy of future monitoring where these species overlap.
Suggested Reviewers:	Diana F. Tomback, Ph.D. Professor, University of Colorado Denver College of Liberal Arts and Sciences diana.tomback@ucdenver.edu Diana Tomback is a leading researcher on the ecology, conservation, and restoration of five-needle white pines in western North America.
	Elizabeth Pansing, Ph.D. Director, Forest and Restoration Science, American Forests Inc epansing@americanforests.org Elizabeth Pansing has researched whitebark pine ecology and management as well as

	alpine and subalpine forests and she has used FIA data for whitebark pine modeling. Melissa Jenkins Whitebark Pine Ecosystem Foundation melissa.jenkins@whitebarkfound.org Melissa Jenkins is experienced in whitebark pine silviculture, management, and recovery.
Opposed Reviewers:	
Response to Reviewers:	Author response to comments We thank the Editor, Associate Editor, and Reviewers for their helpful comments, which allowed us to substantively improve this manuscript. We have reorganized the previously combined Results/Discussion section to include separate results and discussion, with a subsection for "Implications for users of FIA data" and a concise "Conclusions" subsection in the discussion. We also incorporated changes to address each specific comment, as described below. Each Editor/Reviewer comment is listed followed by our response with updated line numbers. Comments from the Editors and Reviewers: Editor in chief: The suggested revisions are a bit more extensive than I typically allow for this decision, so I gave you an extra 10 days to address them. Reviewer 2 does suggest separating the results and discussion into two sections; if you take that route, please have the "Conclusions" as a subsection within the discussion (the suggested title "Management Implications" is fine). Response: Thank you for the additional time and for providing clarity on the recommendation to separate results and discussion. We have reorganized the paper as suggested, and we agree that this flow and organization is improved. For Table 2, I would prefer a setup more aligned with a traditional table. You could display most of that information in 7 columns; as long as provide the total sample size, I think the actual confusion matrix can be calculated from the 5 summary metrics you already provide. Response: We appreciate this suggestion for improved presentation clarity and have modified the format of Table 2 as suggested. Associate Editor: The paper is refreshingly well-written with a clear purpose, appropriate methods, and well reasoned conclusions. The reviewers have made some suggestions for further improvement, which I recommend the authors consider before finalizing the paper. Some minor editorial suggestions: - insert a space between values and units (e.g., "2100m" line 351 and elsewhere) Response: Thank you for noting the strengths of the paper as well as the need to properly space values relative to units. We have made this change throughout the manuscript. - figure captions seem very long. is it possible to condense? Response: We condensed the captions and took out some redundancy in the alternative text (e.g. restating of results and methods that are discussed in the manuscript). - is there room to insert a map of the USA to indicate the position of the study area within the country? For. Sci. is an international journal, and we should do our best to make this clear in illustrations. Response: We have added a location map of North America that highlights the Rocky Mountain Research Station and our study area (see Figure 1).

Reviewer #1: This paper covers an important topic. It is well-structured and easy to follow.
The problem and objectives are well-stated.
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The paper investigates how well FIA field crews are able to differentiate whitebark pine and limber pine, which are similar in needle and tree growth form characteristics and overlap in elevation and some site types. The study focuses on FIA plot locations where whitebark pine and limber pine overlap in the Rocky Mountains. It takes advantage of five-needle pine needle tissue collections from FIA plots, originally intended for other purposes, which were then genetically analyzed comparing two different chloroplast loci which can conclusively distinguish whitebark and limber pine. Correctly identifying whitebark pine to determine where it occurs has become particularly important since its federal listing as a threatened species was announced in 2022 (but effective in 2023). The listing has increased interest in the species and various modeling efforts, particularly with respect to climate change and the impact of several threats.

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Response: These are important points that we attempted to be more transparent about in the revised manuscript. In the Discussion, we acknowledge that verifying the true range of these species' overlap would require a much larger sample size than we used in this analysis (see L494-497).

The structure of the paper is a little unusual in that results and discussion are combined. In order to emphasize the critical points, I would suggest a "General Discussion" section instead of "Implications for users of FIA data" that encompasses some individual points brought up and then a concluding "Management Implications" section rather than a "Conclusions" section, which includes the material currently in "Conclusions" but may expand and bring additional points in. The identification issue is not just a problem for FIA data but for survey and monitoring purposes and especially for determining distributional data. Also, problems with identification may occur for FIA and monitoring data in other areas of overlap between species of five-needle white pines especially for distinguishing pre-reproductive age classes, e.g., including western white pine and whitebark pine, although the needle traits are a little more distinctive but

not always clear. This analysis and concern about data quality thus have implications beyond the single issue of distinguishing non-reproductive whitebark and limber pine.

Response: We appreciate the suggestion to reorganize the paper with separate Results and Discussion sections, and we have made this change. Additionally, we added language to the Conclusions to highlight that our findings may be useful not just for FIA data collection but for any studies that rely on field-based species identification (L489-490, L423-425).

It is important to mention early in the introduction that seeds of both trees are primarily disseminated by Clark's nutcracker but fallen limber pine seeds may be cached locally by small mammals and jays. Nutcracker caches of both pine species may be raided by granivorous rodents (e.g., Pansing et al. 2017) and secondarily cached. Nutcrackers will cache seeds only a few meters from source trees as well as flying seeds to a max of 32 km (Tomback 1978, Lorenz et al. 2011). The implications of nutcracker seed dispersal (e.g., Tomback et al. 2011) is that the bird can disseminate seeds far from seed sources and in different forest types which Goeking et al. (2019) confirmed using FIA data. This perspective may have bearing on the challenges posed by five-needle pine identification. The section beginning L33 is confusing to a reader who is not aware of this information.

Response: Thank you for this helpful information about dispersers and how their different dispersal characteristics affect the distribution of these tree species. We have revised this paragraph to incorporate the information you shared (see L33-43).

Regarding Table 3 results, L204 in the Methods does not explain the use of Chi-square in Cramer's V scores, with which many readers may be unfamiliar.

Citation/explanation? The caption for Table 3 alludes to it. This needs to be better addressed in both places.

Response: We added a brief explanation of Cramer's V scores as an indication of the strength of relationships among two categorical variables such as when using chi-square tests (see L214-215 and Table 3).

There are alternative legends presented for the figures and tables. Some are very long with shorter alternative versions. If more information were in the text, the legends could state "see text for details."

Response: We have shortened the figure legends and alternative text. We aimed to reduce redundancy between manuscript and the figure legends and alternative text. We maintained informative alternate text for readers who may not be able to visually interpret information presented solely in the figures.

The paper in general is generally well-written, but there are a number of places where alternative wording would clarify a statement or procedure, and some of the methods presented are confusing. For example, under Materials and Methods, the needle sampling protocol, i.e., how many samples per plot and how selected, needs to be clearer. They are listed below.

Response: Thank you for your attention to clarity. We have implemented each of your helpful suggestions, as described below.

Abstract

L3. Rather than "vegetative similarities," try morphological similarities. Vegetative preferred definition is plant growth.

Response: We appreciate this suggestion and have made this change (see Abstract, L3).

Study Implications: Please modify the last sentence. "These results demonstrate reliability of FIA for whitebark pine assessment...." The authors use reliability here as a qualitative measure but the casual reader may interpret the sentence as "the data are reliable."

Response: We revised this to "These results quantify reliability..." (see Study Implications, L7-8)

Introduction

L9-19, "decline" is used 6 times in this paragraph and needs alternative wording. Try L11 "...with higher rates of loss in recent years..." Try L16, "Because of these on-going threats...", or something similar.

Response: Thank you for pointing out this redundancy. We incorporated the suggested changes and reduced the use of 'decline' to two times in this paragraph (see L9-19).

L21, "However, the similarity..use between not of....

Response: We have made this change (see L21).

L22, instead of "overall morphology," use growth form.

Response: We have made this change (see L22).

L 25, not "structure" but morphology.

Response: We have made this change (see L25).

L27-28, instead of "branch dieback"—not clear: use branch death or canopy kill.

Response: We have clarified that 'dieback' means 'branch death' (see L27-28).

L33-45, this paragraph needs work and more clarity. Nutcrackers are the dispersal agent likely to bring limber and whitebark pine seeds into disturbed areas. As a caveat, nutcrackers will cache seeds near seed source trees and also transport seeds several to many kilometers for seed caching.

Rodents occupy territories and would not range very far outside to gather cones. This sentence needs work—my edits: "The challenge of identifying young trees is exacerbated in disturbed areas, where both tree species may be pioneering, and in other forest types without five-needle white pines in the overstory." In both situations, long-distance seed dispersal by Clark's nutcrackers may lead to whitebark pine or limber pine regeneration in these community types if conditions are suitable.

Not sure which "other dispersal agents" the authors are referencing in the paragraph; none transport seeds over large distances, but rodents can locally re-cache seeds originally cached by nutcrackers and other rodents. Stellar's jays are territorial and do not transport more than a few seeds at a time and not over long distances. The authors should specifically mention findings in the Goeking et al. (2019) paper which also uses FIA data to make their point about whitebark pine regeneration in different forest communities.

Response: Thank you for your feedback and suggestions throughout this paragraph, and particularly the important contextual information about the various disperser species. To address these comments, we implemented the wording you kindly suggested. Additionally, we have made the following changes: First, we added 'up to' ('...typically disperse seeds up to a few kilometers away') to address that seeds are often cached near seed source trees (see L38). Second, we incorporated the suggested changes in lines 33-36 (now L34-37). Third, we removed the reference to 'other dispersal agents'. We also referenced the findings of Goeking et al. (2019) and other papers using FIA data to reach the same conclusion (see L42-43).

L44, Papers that demonstrate overlap at high elevations between whitebark and limber pine in the Rocky Mountains: Resler and Tomback (2008), AAAR and Tomback et al. (2014), AAAR. Referencing "the species" in this paragraph became confusing—maybe call out whitebark pine and limber pine here.

Response: We clarified statements that referred to one or both species throughout this paragraph. Thank you for the additional citations; we have revised the citations for this

statement (see L46-47).

L48, plots actually moved? Or relocated or established?

Response: Thank you for pointing the ambiguity of our original language. The guidance in the cited protocol states that if "...you cannot, with 100% confidence, verify which trees on the plot are whitebark, select an alternate plot from the list provided to sample." We have adjusted our wording to better reflect the language in the protocol (see L50-51).

L49-54, First, in reality up to Alongi et al. (2019), no reliable method was available for telling pre-reproductive age classes of whitebark and limber pine apart. Second, as implied, the importance of distinguishing whitebark and limber pine apart for every age class varies with the objectives of the monitoring or survey. If not distributional than not as critical. Resler and Tomback (2008) applied the needle morphology differences noted by Kral, R. (1993) (Pinus. In Flora of North America Editorial Committee, 1993, Flora of North America North of Mexico, Vol. 2. New York and Oxford: Oxford University Press) which seemed to work sufficiently in their study area (but no control) but requires hand lens or dissecting microscope and specific knowledge.

Response: Thank you for drawing attention to this paragraph. We were not intending to disparage any of the described methodologies, as they were designed to meet study objectives and use available resources. We have added some additional text to this paragraph to acknowledge the utility of these methods while also explaining why incorporating new resources (the test detailed in Alongi et al. 2019) is necessary for the type of sample design used by FIA (see L56-60). Additionally, we have referenced the methodology used by Resler and Tomback (2008) (see L55-56).

L95, 97, "approximately" implies nearly equal to. Is another term better to use here?

Response: In the first instance, we use "approximately" (now L101) because although this seems to be an exact number, some plots represent more or less area, based on FIA estimation procedures or plot placement (e.g., plots that land on the edge of the RMRS region). We did not include this level of detail, though specifics can be found in the cited references. In the second instance, we removed the word "approximately" because we do aim to sample exactly 10% of plots each year. The actual percentage varies due to circumstances that may temporarily prevent plot measurement (e.g. pandemic related travel restrictions). To account for this, we have clarified that 10% of FIA plots 'are targeted' for visit each year (see L103-104).

L99, what is the FIA plot size or range of sizes?

Response: Plot size is always the same. We now report the size to the nearest square meter (see L105).

L100, need spaces around symbols $\geq$ and units of measurement. Where is the diameter measured? Is it DBH?

L102, DBH? clarify diameter limits and where measured.

Response: Thank you for drawing our attention to this formatting. We have fixed the symbol and unit spacing throughout the document. We now refer to 'diameter' throughout the paragraph because we are referencing the FIA protocol, which pertains to species that have diameters measured at breast height and root collar (L105-111). We added a sentence at the end of the paragraph to clarify that diameter is taken at breast height for whitebark and limber pine (see L109-111).

L105-111. The sampling protocol is confusing. You start out stating "one tissue sample consisting of at least five needles from one individual..." Can you clarify the decision flow of how many sample to collect, and how many needle samples and how distributed among plots, subplots etc.?

Response: Thank you for pointing out where we need to clarify our protocol. We have revised both individual sentences and the order of statements in the paragraph to provide a clearer description (see L113-122).

L114-115, "conclusively identified" through the genetic methods? Please provide information.

Response: We clarified that these samples had conclusive genetic test results (i.e. DNA successfully extracted, no contamination, etc.) (see L123).

L154, define "false positive error rates."

Response: We provide a citation (James et al. 2013), a formula, and a narrative description of false positive error rates in the text immediately following the formula (see L162, L164, and L167-168).

L167-175. Why is Table 3 cited after Table 1? Unless I missed something, Table 3 should be converted to Table 2.

Response: Thank you for noticing this. We have modified the text to refer to Table 3 in the Results, after Table 2 is introduced, and edited the Methods to not refer to Table 3.

L198-199, "how misidentifications may affect occurrence patterns..." It strikes me that this is a derivative piece of information. The predictor variables and modelling indicate which factors are more likely to lead to misidentifications.

Response: Thank you for noticing this ambiguous word choice. We changed this sentence to "We compared field- versus lab-identified whitebark pine presence across different predictor variable values or categories to better understand the circumstances in which misidentification is most likely to occur." (see L208-210).

L208-209. This needs be rewritten. It is accuracy that comes from cumulative experience; "cumulative accuracy" is not a good descriptor for this situation.

Response: Thank you for careful consideration of our word choice. Rather than changing the descriptor, we clarified the definition of "cumulative accuracy," because it does indeed refer to the mean accuracy of all samples collected by a crew leader over time. For example, if a crew leader collected one sample and incorrectly identified it on their first plot, they would have a cumulative accuracy of 0% (0 out of 1 samples correctly identified). If they correctly identified 2 samples on their second plot, their cumulative accuracy would increase to 67% (2 out of 3 samples correctly identified). We hope this methodology is now sufficiently clear in the manuscript and reflects the example provided here. Please see L220-221 (Methods) and L268-269 (Results).

Results

L219, Table 2 should be renamed Table 3 because of the order of reference (see above).

Response: We removed the earlier reference to Table 3, as that reference did not add substantive value to the Methods section. Thus, the original table numbering has not changed, and the order of reference matches the numbering.

L221-225. The explanation differentiating seed dispersal by nutcrackers in whitebark pine and limber pine is very speculative and should be eliminated. Limber pine seeds are often dispersed long distances by nutcrackers (Lanner and Vander Wall 1980, Williams et al. 2020). I would focus on the fact that the whitebark pine cones are less persistent on trees because they are deconstructed in the process of seed removal, but we often find remnants of previous years' cones on whitebark pine trees—to the point they confuse novices about new cones when we do cone counts. Limber pine may have several years' of old cones remaining on trees, which in fact makes it easier to assign tree identity.

Response: Thank you for drawing attention to this. We removed the speculative explanation and focused on the effects of cone persistence (see L342-351).

L243-248, this explanation might be better served where the two models are described

under Methods.

Response: We moved this explanation to the Methods section (see new location at L202-206, and L243-245).

L249-260. Should probably refer back to Table 1 again for the factors listed.

Response: Thank you for noting this linkage. We added a reference to Table 1 (see L235-236, L248).

L283, not "between" but among (3 or more).

Response: We have made this change (see L278).

L285-289, see comments above about Chi-square (sometimes capitalized in paper, sometimes not) and Cramer's V scores.

Response: We have revised all occurrence of chi-square to be lower case. Additionally, we added an explanation of Cramer's V scores, their relation to chi-square tests (see L214-216).

L293, "often leaving no evidence of cones afterward..." I would state small remnants or no evidence.

Response: We have made this change (see L346).

L334, Indent, new paragraph.

Response: We have created a separate paragraph to discuss the relationship of habitat type and five-needle pines (L308-319). With the reorganization of results and discussion, the suggested paragraph break is now the second sentence of the paragraph (L310).

L 356, "...shift in limber pine elevation suggests...." not means.

Response: Thank you for your attention to this language. We have made this change (see L326).

L382-383, this sentence is not clear. Please state more simply—it is important.

Response: We have revised this sentence and also moved it to the end of the paragraph to better indicate that these FIA-specific error rates likely extend beyond our results to other monitoring datasets (see L423-425).

L436, clarify writing--not "contain" but include only...

Response: We have made this change (see L473).

L453, clarify this suggestion: "First, sample protocols can target...." Should prioritize?

Response: We agree "should prioritize" is clearer and made this change (see L490-491).

L457, rewrite: "targeted training" not clear. Training that emphasizes distinguishing whitebark pine from limber pine...?

Response: We revised these sentences to add some clarity to the purpose and content of suggested training, and remove the phrase 'targeted training' (see L497-L502).

L452-462, Rolling in all these factors such as forest type and habitat type, etc. may help improve accuracy. This would be worth studying. The only definitive approach is to use the genetic method.

Response: We clarified that crews should be trained to rely on these factors for

	identification only when verification via other methods (i.e. cones, genetic analysis) is not possible (see L497-L500). We agree that studying the effects of training on accuracy would be valuable, and more genetic sampling by trained employees is necessary to do so (see L503-506). L463-467, more accuracy in distinguishing the two species is also important for any modelling regarding seedling niches or climate change predictions. Response: Thank you for drawing our attention to this area, as our original phrasing obscured the paragraph topic. This paragraph was intended to focus on the relationship between genetic sampling and training, specifically how improved understanding of occurrence could improve field identification (which, as mentioned in the previous comment, will be worth studying as data becomes available). The benefits of more accurate identification are numerous, and we have tried to address them throughout the paper. We have re-written this section to clarify the focus (see L503-506), and we specifically mention the benefits for seedling niche and climate change projections in lines 509-511. L486, instead of targeted training, which is jargony, it would be more details training that integrates multiple factors to distinguish between the species. Response: Thank you for this suggestion. We have changed this sentence to read '...crews that are trained to use multiple factors for species identification' (see L529).	
Additional Information:		
Question	Response	
Please enter the Word Count of your manuscript	7604	
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Author response to comments

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Response: Thank you for this helpful information about dispersers and how their different dispersal characteristics affect the distribution of these tree species. We have revised this paragraph to incorporate the information you shared (see L33-43).

Regarding Table 3 results, L204 in the Methods does not explain the use of Chi-square in Cramer's V scores, with which many readers may be unfamiliar. Citation/explanation? The caption for Table 3 alludes to it. This needs to be better addressed in both places.

Response: We added a brief explanation of Cramer's V scores as an indication of the strength of relationships among two categorical variables such as when using chi-square tests (see L214-215 and Table 3).

There are alternative legends presented for the figures and tables. Some are very long with shorter alternative versions. If more information were in the text, the legends could state "see text for details."

Response: We have shortened the figure legends and alternative text. We aimed to reduce redundancy between manuscript and the figure legends and alternative text. We maintained informative alternate text for readers who may not be able to visually interpret information presented solely in the figures.

The paper in general is generally well-written, but there are a number of places where alternative wording would clarify a statement or procedure, and some of the methods presented are confusing. For example, under Materials and Methods, the needle sampling protocol, i.e., how many samples per plot and how selected, needs to be clearer. They are listed below.

Response: Thank you for your attention to clarity. We have implemented each of your helpful suggestions, as described below.

Abstract

L3. Rather than "vegetative similarities," try morphological similarities. Vegetative preferred definition is plant growth.

Response: We appreciate this suggestion and have made this change (see Abstract, L3).

Study Implications: Please modify the last sentence. "These results demonstrate reliability of FIA for whitebark pine assessment...." The authors use reliability here as a qualitative measure but the casual reader may interpret the sentence as "the data are reliable."

Response: We revised this to "These results quantify reliability..." (see Study Implications, L7-8)

Introduction

L9-19, "decline" is used 6 times in this paragraph and needs alternative wording. Try L11 "...with higher rates of loss in recent years..." Try L16, "Because of these on-going threats...", or something similar.

Response: Thank you for pointing out this redundancy. We incorporated the suggested changes and reduced the use of 'decline' to two times in this paragraph (see L9-19).

L21, "However, the similarity..use between not of....

Response: We have made this change (see L21).

L22, instead of "overall morphology," use growth form.

Response: We have made this change (see L22).

L 25, not "structure" but morphology.

Response: We have made this change (see L25).

L27-28, instead of "branch dieback"—not clear: use branch death or canopy kill.

Response: We have clarified that 'dieback' means 'branch death' (see L27-28).

L33-45, this paragraph needs work and more clarity. Nutcrackers are the dispersal agent likely to bring limber and whitebark pine seeds into disturbed areas. As a caveat, nutcrackers will cache seeds near seed source trees and also transport seeds several to many kilometers for seed caching.

Rodents occupy territories and would not range very far outside to gather cones. This sentence needs work—my edits: "The challenge of identifying young trees is exacerbated in disturbed areas, where both tree species may be pioneering, and in other forest types without five-needle white pines in the overstory." In both situations, long-distance seed dispersal by Clark's nutcrackers may lead to whitebark pine or limber pine regeneration in these community types if conditions are suitable.

Not sure which "other dispersal agents" the authors are referencing in the paragraph; none transport seeds over large distances, but rodents can locally re-cache seeds originally cached by nutcrackers and

other rodents. Stellar's jays are territorial and do not transport more than a few seeds at a time and not over long distances. The authors should specifically mention findings in the Goeking et al. (2019) paper which also uses FIA data to make their point about whitebark pine regeneration in different forest communities.

Response: Thank you for your feedback and suggestions throughout this paragraph, and particularly the important contextual information about the various disperser species. To address these comments, we implemented the wording you kindly suggested. Additionally, we have made the following changes: First, we added 'up to' ('...typically disperse seeds up to a few kilometers away') to address that seeds are often cached near seed source trees (see L38). Second, we incorporated the suggested changes in lines 33-36 (now L34-37). Third, we removed the reference to 'other dispersal agents'. We also referenced the findings of Goeking et al. (2019) and other papers using FIA data to reach the same conclusion (see L42-43).

L44, Papers that demonstrate overlap at high elevations between whitebark and limber pine in the Rocky Mountains: Resler and Tomback (2008), AAAR and Tomback et al. (2014), AAAR. Referencing "the species" in this paragraph became confusing—maybe call out whitebark pine and limber pine here.

Response: We clarified statements that referred to one or both species throughout this paragraph. Thank you for the additional citations; we have revised the citations for this statement (see L46-47).

L48, plots actually moved? Or relocated or established?

Response: Thank you for pointing the ambiguity of our original language. The guidance in the cited protocol states that if "...you cannot, with 100% confidence, verify which trees on the plot are whitebark, select an alternate plot from the list provided to sample." We have adjusted our wording to better reflect the language in the protocol (see L50-51).

L49-54, First, in reality up to Alongi et al. (2019), no reliable method was available for telling pre-reproductive age classes of whitebark and limber pine apart. Second, as implied, the importance of distinguishing whitebark and limber pine apart for every age class varies with the objectives of the monitoring or survey. If not distributional than not as critical. Resler and Tomback (2008) applied the needle morphology differences noted by Kral, R. (1993) (Pinus. In Flora of North America Editorial Committee, 1993, Flora of North America North of Mexico, Vol. 2. New York and Oxford: Oxford University Press) which seemed to work sufficiently in their study area (but no control) but requires hand lens or dissecting microscope and specific knowledge.

Response: Thank you for drawing attention to this paragraph. We were not intending to disparage any of the described methodologies, as they were designed to meet study objectives and use available resources. We have added some additional text to this paragraph to acknowledge the utility of these methods while also explaining why incorporating new resources (the test detailed in Alongi et al. 2019) is necessary for the type of sample design used by FIA (see L56-60). Additionally, we have referenced the methodology used by Resler and Tomback (2008) (see L55-56).

L95, 97, "approximately" implies nearly equal to. Is another term better to use here?

Response: In the first instance, we use "approximately" (now L101) because although this seems to be an exact number, some plots represent more or less area, based on FIA estimation procedures or plot

placement (e.g., plots that land on the edge of the RMRS region). We did not include this level of detail, though specifics can be found in the cited references. In the second instance, we removed the word "approximately" because we do aim to sample exactly 10% of plots each year. The actual percentage varies due to circumstances that may temporarily prevent plot measurement (e.g. pandemic related travel restrictions). To account for this, we have clarified that 10% of FIA plots 'are targeted' for visit each year (see L103-104).

L99, what is the FIA plot size or range of sizes?

Response: Plot size is always the same. We now report the size to the nearest square meter (see L105).

L100, need spaces around symbols $\geq$ and units of measurement. Where is the diameter measured? Is it DBH?

L102, DBH? clarify diameter limits and where measured.

Response: Thank you for drawing our attention to this formatting. We have fixed the symbol and unit spacing throughout the document. We now refer to 'diameter' throughout the paragraph because we are referencing the FIA protocol, which pertains to species that have diameters measured at breast height and root collar (L105-111). We added a sentence at the end of the paragraph to clarify that diameter is taken at breast height for whitebark and limber pine (see L109-111).

L105-111. The sampling protocol is confusing. You start out stating "one tissue sample consisting of at least five needles from one individual..." Can you clarify the decision flow of how many sample to collect, and how many needle samples and how distributed among plots, subplots etc.?

Response: Thank you for pointing out where we need to clarify our protocol. We have revised both individual sentences and the order of statements in the paragraph to provide a clearer description (see L113-122).

L114-115, "conclusively identified" through the genetic methods? Please provide information.

Response: We clarified that these samples had conclusive genetic test results (i.e. DNA successfully extracted, no contamination, etc.) (see L123).

L154, define "false positive error rates."

Response: We provide a citation (James et al. 2013), a formula, and a narrative description of false positive error rates in the text immediately following the formula (see L162, L164, and L167-168).

L167-175. Why is Table 3 cited after Table 1? Unless I missed something, Table 3 should be converted to Table 2.

Response: Thank you for noticing this. We have modified the text to refer to Table 3 in the Results, after Table 2 is introduced, and edited the Methods to not refer to Table 3.

L198-199, "how misidentifications may affect occurrence patterns..." It strikes me that this is a derivative piece of information. The predictor variables and modelling indicate which factors are more likely to lead to misidentifications.

Response: Thank you for noticing this ambiguous word choice. We changed this sentence to "We compared field- versus lab-identified whitebark pine presence across different predictor variable values or categories to better understand the circumstances in which misidentification is most likely to occur." (see L208-210).

L208-209. This needs be rewritten. It is accuracy that comes from cumulative experience; "cumulative accuracy" is not a good descriptor for this situation.

Response: Thank you for careful consideration of our word choice. Rather than changing the descriptor, we clarified the definition of "cumulative accuracy," because it does indeed refer to the mean accuracy of all samples collected by a crew leader over time. For example, if a crew leader collected one sample and incorrectly identified it on their first plot, they would have a cumulative accuracy of 0% (0 out of 1 samples correctly identified). If they correctly identified 2 samples on their second plot, their cumulative accuracy would increase to 67% (2 out of 3 samples correctly identified). We hope this methodology is now sufficiently clear in the manuscript and reflects the example provided here. Please see L220-221 (Methods) and L268-269 (Results).

Results

L219, Table 2 should be renamed Table 3 because of the order of reference (see above).

Response: We removed the earlier reference to Table 3, as that reference did not add substantive value to the Methods section. Thus, the original table numbering has not changed, and the order of reference matches the numbering.

L221-225. The explanation differentiating seed dispersal by nutcrackers in whitebark pine and limber pine is very speculative and should be eliminated. Limber pine seeds are often dispersed long distances by nutcrackers (Lanner and Vander Wall 1980, Williams et al. 2020). I would focus on the fact that the whitebark pine cones are less persistent on trees because they are deconstructed in the process of seed removal, but we often find remnants of previous years' cones on whitebark pine trees—to the point they confuse novices about new cones when we do cone counts. Limber pine may have several years' of old cones remaining on trees, which in fact makes it easier to assign tree identity.

Response: Thank you for drawing attention to this. We removed the speculative explanation and focused on the effects of cone persistence (see L342-351).

L243-248, this explanation might be better served where the two models are described under Methods.

Response: We moved this explanation to the Methods section (see new location at L202-206, and L243-245).

L249-260. Should probably refer back to Table 1 again for the factors listed.

Response: Thank you for noting this linkage. We added a reference to Table 1 (see L235-236, L248).

L283, not "between" but among (3 or more).

Response: We have made this change (see L278).

L285-289, see comments above about Chi-square (sometimes capitalized in paper, sometimes not) and Cramer's V scores.

Response: We have revised all occurrence of chi-square to be lower case. Additionally, we added an explanation of Cramer's V scores, their relation to chi-square tests (see L214-216).

L293, "often leaving no evidence of cones afterward..." I would state small remnants or no evidence.

Response: We have made this change (see L346).

L334, Indent, new paragraph.

Response: We have created a separate paragraph to discuss the relationship of habitat type and five-needle pines (L308-319). With the reorganization of results and discussion, the suggested paragraph break is now the second sentence of the paragraph (L310).

L 356, "...shift in limber pine elevation suggests...." not means.

Response: Thank you for your attention to this language. We have made this change (see L326).

L382-383, this sentence is not clear. Please state more simply—it is important.

Response: We have revised this sentence and also moved it to the end of the paragraph to better indicate that these FIA-specific error rates likely extend beyond our results to other monitoring datasets (see L423-425).

L436, clarify writing--not "contain" but include only...

Response: We have made this change (see L473).

L453, clarify this suggestion: "First, sample protocols can target...." Should prioritize?

Response: We agree "should prioritize" is clearer and made this change (see L490-491).

L457, rewrite: "targeted training" not clear. Training that emphasizes distinguishing whitebark pine from limber pine...?

Response: We revised these sentences to add some clarity to the purpose and content of suggested training, and remove the phrase 'targeted training' (see L497-L502).

L452-462, Rolling in all these factors such as forest type and habitat type, etc. may help improve accuracy. This would be worth studying. The only definitive approach is to use the genetic method.

Response: We clarified that crews should be trained to rely on these factors for identification only when verification via other methods (i.e. cones, genetic analysis) is not possible (see L497-L500). We agree that

studying the effects of training on accuracy would be valuable, and more genetic sampling by trained employees is necessary to do so (see L503-506).

L463-467, more accuracy in distinguishing the two species is also important for any modelling regarding seedling niches or climate change predictions.

Response: Thank you for drawing our attention to this area, as our original phrasing obscured the paragraph topic. This paragraph was intended to focus on the relationship between genetic sampling and training, specifically how improved understanding of occurrence could improve field identification (which, as mentioned in the previous comment, will be worth studying as data becomes available). The benefits of more accurate identification are numerous, and we have tried to address them throughout the paper. We have re-written this section to clarify the focus (see L503-506), and we specifically mention the benefits for seedling niche and climate change projections in lines 509-511.

L486, instead of targeted training, which is jargony, it would be more details training that integrates multiple factors to distinguish between the species.

Response: Thank you for this suggestion. We have changed this sentence to read ‘...crews that are trained to use multiple factors for species identification’ (see L529).

Accuracy of whitebark pine and limber pine identification by Forest Inventory and Analysis field crews

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ABSTRACT:

Accurate identification of whitebark and limber pine has become increasingly important following the 2022 listing of whitebark pine as a threatened species under the Endangered Species Act. However, morphological similarities make identification of the two species difficult where ranges overlap. Using a genetic test that differentiates whitebark and limber pine, we compared field identification by Forest Inventory and Analysis field crews with genetic identification for needle samples from 371 trees. Field identifications were 100% correct for the 76 samples collected from outside regions of species' range overlap. Eighty-three percent of the field identifications were correct in regions of range overlap (89% for large trees, 88% for saplings, and 78% for seedlings). Field-identified samples were correct 60% of the time for limber pine and >99% for whitebark pine. Random forests analysis revealed that identification accuracy is influenced by crew experience, large (≥ 12.7 cm diameter) limber or whitebark pines recorded by field crews on the plot, elevation, Julian day of sample collection, and habitat type. We found that whitebark pine has likely been underestimated, and limber pine overestimated, within their overlapping ranges. We provide insights on improving accuracy of future monitoring where these species overlap.

KEYWORDS: Forest inventory; genetic identification; whitebark pine; limber pine; quality assessment

STUDY IMPLICATIONS:

1 Accurate identification of whitebark pine is critical for monitoring this threatened
2 species, yet distinguishing whitebark from limber pine can be difficult. Genetic analysis
3 determined accuracy of field identification by Forest Inventory and Analysis (FIA) crews was 83%
4 where the species' ranges overlap. Virtually all individuals identified as whitebark pine were
5 genetically confirmed to be whitebark pine, although nearly 40% of individuals identified as
6 limber pine were actually whitebark pine. Thus, previous data underestimated whitebark and
7 overestimated limber pine abundance in the species' range overlap. These results quantify
8 reliability of FIA data for whitebark pine assessments and identify areas for improvement.

INTRODUCTION:

High-elevation five-needle pines, which include whitebark pine (*Pinus albicaulis* Engelm.) and limber pine (*Pinus flexilis* James), play important roles in high-mountain ecosystems across western North America. These species provide a host of ecological and cultural benefits including serving as keystone or foundational species (Tomback et al. 2011), providing wildlife food and habitat, creating and sustaining biodiversity, facilitating succession, regulating snowpack melt and runoff, reducing soil erosion, and contributing to aesthetic and spiritual values (Steele 1990; Tomback et al. 2001; Tomback and Achuff 2010; Tomback et al. 2011; Windmuller-Campione and Long 2016).

Declines in whitebark and limber pine have been observed throughout most of their ranges over the past several decades (Tomback et al. 2001; Tomback et al. 2011; Goeking and Izlar 2018; Goeking and Windmuller-Campione 2021; Burns et al. 2023), with higher mortality rates in recent years (Goeking and Windmuller-Campione 2021; Burns et al. 2023). White pine blister rust (caused by *Cronartium ribicola* Fisch.), mountain pine beetles (*Dendroctonus ponderosae* Hopkins), altered fire regimes, forest succession, climate change, and interactions among these factors have caused declines in both species (Gibson et al. 2008; Tomback and Achuff 2010; Campbell et al. 2011; Tomback et al. 2011; Cleaver et al. 2015; Keane et al. 2022; Burns et al. 2023). Because of these ongoing threats, whitebark pine was listed as threatened under the Endangered Species Act by the US Fish and Wildlife Service in December 2022 (US Fish and Wildlife Service 2022). Goeking and Windmuller-Campione (2021) noted that limber pine population trends are comparable to the trends exhibited by whitebark pine less than 10 years earlier.

Reliable inventory data are required for scientific studies and for monitoring the status of these species (Keane et al. 2022; Tomback and Sprague 2022). However, the similarity between whitebark and limber pines' needles, bark, and growth form make it very difficult to distinguish the two species based on vegetative characteristics alone (Arno and Hammerly 2007; Alongi et al. 2019; Hansen et al. 2021). When present, pollen and seed cones of whitebark and limber pine are sufficiently distinct in color,

morphology, and persistence that the two species can be reliably distinguished (Arno and Hoff 1989; McCaughey and Schmidt 2001; Lesica 2012). However, cone-bearing trees of both species are absent from many sites due to widespread mortality (Tomback and Achuff 2010; Keane et al. 2022), branch dieback (i.e., branch death) caused by white pine blister rust (McKinney and Tomback 2007; Tomback and Achuff 2010; Cleaver et al. 2015), seed predation, and unsuitable weather conditions (Hansen et al. 2021). Additionally, these slow-growing species can take 20-40 years to produce cones, and large cone crops do not typically occur in whitebark pine until trees are at least 60 to 80 years old (Krugman and Jenkinson 1974; Arno and Hammerly 2007). Thus, cones are often absent from younger trees.

The challenge of identifying young trees is exacerbated in disturbed areas, where both species may be pioneering, and in other forest types without five-needle pines in the overstory. In both circumstances, long-distance seed dispersal by Clark's nutcrackers (*Nucifraga columbiana* Wilson) may lead to whitebark pine or limber pine regeneration in these community types if conditions are suitable (Tomback and Linhart 1990; Lorenz et al. 2011; Tomback et al. 2011). Nutcrackers typically disperse seeds up to a few kilometers, routinely transport seeds 12 to 22 km (Tomback and Linhart 1990), and may disperse seeds as far as 32 km (Lorenz et al. 2011), often over large elevation gradients (Tomback and Linhart 1990; Lorenz et al. 2011; Tomback et al. 2011). This dispersion results in regeneration of whitebark and limber pines on sites that may not have trees of these same species in the overstory (Windmuller-Campione and Long 2016; Goeking and Izlar 2018; Goeking et al. 2019; Goeking and Windmuller-Campione 2021). Climate and substrate are also unreliable indicators for species identification, as their effects on species occurrence vary geographically (Arno and Weaver 1990; Hansen-Bristow et al. 1990; McCaughey and Schmidt 2001; Weaver 2001). Additionally, co-occurrence and elevational overlap between whitebark and limber pines has been documented in many areas (Arno and Hoff 1989; Weaver 2001; Resler and Tomback 2008; Hansen et al. 2021).

48 The need to better understand these declining and important species has led to several
49 approaches for addressing identification challenges. For example, some regional monitoring protocols
50 require crews to establish plots in alternate locations if whitebark and limber pine cannot be
51 distinguished in the field at the initial plot location (Greater Yellowstone Whitebark Pine Monitoring
52 Working Group 2011). Whitebark and limber pines are lumped as ‘high-elevation five-needle pines’ in
53 results from USDA Forest Service, Forest Health Protection aerial surveys (Hayes 2016). Tomback et al.
54 (2005) required field crews to be familiar with cone-based species identification in geographic areas with
55 both species, and Resler and Tomback (2008) used needle morphology to distinguish the two species,
56 which requires specialized equipment and knowledge. These methods ensure certain levels of data
57 quality, meet study objectives, and use available resources for identification. However, these approaches
58 are not realistic or reliably effective for field campaigns using probability-based species-specific sampling
59 for all tree ages and species, and new resources (i.e. the genetic testing method detailed in Alongi et al.
60 2019) have recently become available.

61 USDA Forest Service Forest Inventory and Analysis (FIA) conducts a probability-based, statistically
62 representative sample of whitebark and limber pine occurrence that is frequently used for modeling
63 species distribution and responses to climate change (e.g., Bell et al. 2014; Schoettle et al. 2022; Warwell
64 et al. 2006; Windmuller-Campione and Long 2016). FIA data constitute the primary data source
65 throughout whitebark pine’s range in the US and were cited in the decision to list whitebark pine as
66 threatened (US Fish and Wildlife Service 2022). FIA data continue to be used by the US Forest Service to
67 assess impacts of management on whitebark pine and by researchers who are developing future range
68 projections that will guide restoration efforts. This ongoing reliance on FIA data for whitebark pine
69 assessments assumes that species identification is accurate. Although FIA conducts expert checks for
70 quality control (Gray et al. 2012), in situ quality control is hampered when species cannot be conclusively
71 identified in the field. To improve quality control, we analyzed an existing sample of whitebark and

limber pine needles collected from FIA plots using an economical genetic test that differentiates the two species (Alongi et al. 2019).

The objectives of this study were to: (1) assess identification accuracy for whitebark pine and limber pine by Rocky Mountain Research Station (RMRS)-FIA field crews; (2) identify factors that predict when misidentification is most likely to occur; and (3) describe steps that can improve future FIA identification of these two species. We hypothesized that difficulty in distinguishing whitebark and limber pine when cones are absent would lead to misidentification, and we predicted that these errors would be more common for seedlings. By examining patterns in misidentification, we identified additional causes of identification errors and provide recommended procedures to improve future data quality.

MATERIALS AND METHODS:

Study Area

Our study area encompassed regions of whitebark and limber pine range overlap within the states of Montana, Idaho, Wyoming, and Nevada. To define these regions, we first created comprehensive range maps for each species. Maps were built by joining location data from FIA plots containing whitebark and limber pine (as described in Burrill et al. 2023) with digitized range maps developed by the Whitebark Pine Ecosystem Foundation (2014 and 2019) and USDA Forest Service, Forest Health Protection (Forest Health Technology Enterprise Team 2023). We applied a 35 km buffer around each comprehensive range map to encompass the maximum seed dispersal distance of Clark's nutcrackers (Lorenz et al. 2011). Using the intersect tool in ArcGIS, we isolated the area where the buffered ranges overlap. Lastly, we eliminated any areas that fell outside the footprint of RMRS-FIA (Figure 1). The resulting area excluded range overlap in central and southern Sierra Nevada in California, the Wallowa Mountains of northeastern Oregon, and a band that runs through southeastern British Columbia and southwestern Alberta to about 54° north (Tomback et al. 2011). The area of species' range

overlap, hereafter referred to as the study area, covered approximately 75% of whitebark pine range within the RMRS-FIA data collection states and included 89% of RMRS-FIA plots with whitebark pine trees (> 12.7 cm diameter). Fifty percent of limber pine range within the RMRS-FIA data collection states and 50% of RMRS-FIA plots with limber pine trees (> 12.7 cm diameter) were in the study area.

Data collection on FIA plots

The FIA plot grid consists of approximately one plot per 2,428 ha, comprising a probability-based, statistically representative sample across all land cover types, forest types, and ownership groups (Bechtold and Patterson 2005; Burrill et al. 2023). Each year, 10% of FIA plots within the RMRS-FIA footprint are targeted for visit and numerous site, stand, and tree variables are measured (USDA 2010). Each FIA plot consists of four 7.3 m radius subplots, covering 672 m² total. All standing live and dead trees ≥ 12.7 cm diameter (hereafter referred to as ‘large trees’) in the subplot are identified to species and numerous measurements are taken. Nested within each subplot is a 2.1 m radius microplot, wherein field crews measure all saplings (≥ 2.5 cm and < 12.7 cm diameter) and record the number of seedlings per species (*Pinus* spp. seedlings are < 2.5 cm diameter and > 15.2 cm height) (USDA 2010). Diameters are measured at breast height (1.37 m above ground level) for whitebark pine and limber pine (see USDA 2010 for more detail).

Needle samples

From 2010 to 2012, RMRS-FIA field crews identified all tree species present on each subplot and collected one tissue sample per species from the subplot. Samples were collected from individuals with the following order of preference: 1) large trees on the subplot or saplings on the microplot; 2) seedlings on the microplot; 3) large trees immediately adjacent to the subplot or saplings and seedlings located off the microplot but on the subplot; 4) saplings or seedlings immediately adjacent to the subplot. This method resulted in at least one sample for each field-identified species found on each plot, with a maximum of four samples for each species per plot. Each five-needle pine sample consisted of at least

one fascicle of five needles. Samples were placed in envelopes with a small amount of silica gel cat litter and stored in cardboard boxes at the RMRS-FIA lab in Ogden, UT until 2020. Although all species were sampled, this study opportunistically used samples from field-identified whitebark and limber pines.

A total of 371 samples from 205 plots had conclusive genetic test results. Of these, 295 samples were collected from 165 plots located within our study area (Figure 1). These 295 samples represent about 2% of the live whitebark and limber pine trees, saplings, and seedlings measured on FIA plots located within the study area. The field identifications of the remaining 76 samples collected outside of the study area were verified as 100% accurate using the genetic identification tool described below and were therefore excluded from our analyses of identifications errors.

Accuracy of species identification

To test species identification by field crews, genetic analyses were conducted in 2020 and 2021 by the Plant Sciences and Plant Pathology Department lab at Montana State University using the genetic identification tool detailed in Alongi et al. (2019). This tool uses two chloroplast loci to expeditiously distinguish needle samples of whitebark and limber pine trees. This approach is justifiable, as opposed to a genomic approach, for several reasons. The first is that introgressive hybridization between these two species is not known to occur. Ericson (1965), Bingham (1973), and Critchfield (1986) report cursory to uncertain evidence for whitebark and limber pine putative hybrids, either from single trees or small population samples, and these include results from artificial crosses. These studies provide no evidence of introgressive hybridization between whitebark and limber pine. Second, evidence of introgression between species typically involves delimitation of a hybrid zone that lies in the region of contact between the geographical distributions of two putative parental species, as exemplified by limber pine and southwestern white pine (*Pinus strobiformis* Engelm.; Menon et al. 2018) and whitebark pine and sugar pine (*Pinus lambertiana* Douglas; Liston et al. 2007). No such hybrid zone has been detected in the region of overlap for whitebark and limber pine (e.g., as mapped by Little 1971; Ulrich 2023). Within this

region of overlap, Alongi et al. (2019) and follow-up analyses found complete congruence between limber and whitebark pine trees identified using seed-cones and chloroplast haplotypes and these comparisons mostly involved blind tests. Thirdly, our approach would be excessively encumbered by a genomic approach to distinguishing whitebark and limber pine. Genomic analyses have been performed on limber pine (Liu et al. 2016a) and whitebark pine (Liu et al. 2016b; Syring et al. 2016). However, both limber and whitebark pine have large genomes (30.5 Gbp (Liu et al. 2016a) and ~27 Gbp (Syring et al. 2016)) that could not be affordably analyzed at a population level (Syring et al. 2016).

We determined the species identification accuracy for each sample by comparing the field identification written on the sample envelope (referred to as 'field-identified') to the genetic identification (referred to as 'lab-identified'). Accuracy was then calculated as the percentage of samples that were correctly identified. Of the 295 study area samples, 181 were sampled from large trees, saplings, or seedlings that were measured as a standard part of plot data collection (categorized as 'tally' samples), and 114 were sampled from large trees located off the subplot or saplings or seedlings located off the microplot ('non-tally').

To further understand patterns in misidentification, we created a confusion matrix containing data from all samples, and for each size class (seedlings, saplings, large trees, and unknown size). Confusion matrices display 'actual' versus 'predicted' values for two or more classes (in this study lab-identified vs. field-identified) and identify errors of commission and omission. For each confusion matrix, we calculated false positive error rates, sensitivity, and specificity (James et al. 2013) for both whitebark and limber pine:

$$\text{False positive error rate} = \frac{n_{\text{false positives}}}{n_{\text{false positives}} + n_{\text{true positives}}}$$

$$\text{Sensitivity} = \frac{n_{\text{true positives}}}{n_{\text{true positives}} + n_{\text{false negatives}}}$$

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$$Specificity = \frac{n_{true\ negatives}}{n_{true\ negatives} + n_{false\ positives}}$$

False positive error rates identify errors of commission (Type 1 error), e.g., the proportion of limber pine trees that are incorrectly field-identified as whitebark pine. In our study, sensitivity for a species indicates the ability of FIA field crews to correctly field-identify a sample that is lab-identified as that species. Specificity for a given species indicates the field crews' ability to correctly field-identify a sample that is not the given species (i.e., it is lab-identified as the other species). Because our study examined only two species, the specificity of one species was equal to the sensitivity of the other.

Predictors of identification accuracy

To identify predictors of misidentification errors, we developed a list of 12 potential predictors based on guidance given to RMRS-FIA field crews and on a literature review (Table 1). These predictors were grouped into three types of variables: 1) observer-related variables; 2) tree-level variables associated with the presence of cones; and 3) site-level variables that influence species distribution patterns or the likelihood of encountering both species (Table 1).

Crew leader experience was calculated as the number of plots with whitebark or limber pine in the study area that a crew leader had measured at the time of sample collection. We aggregated habitat type, which describes the potential (late seral or climax) natural vegetation based on climate, geography, or other site characteristics (Pfister et al. 1977), to the series level (Burrill et al. 2023) resulting in five habitat type series. We aggregated field-recorded forest type (i.e., FLDTYPCD in Burrill et al. 2023), which indicates the predominant live tree species or group of species in the stand (USDA 2010), to six forest-type groups (Burrill et al. 2023). Whitebark pine seed zones defined by Mahalovich and Hipkins (2011) encompass areas of similar environmental conditions and allowed comparison of accuracy rates among areas differing in geology, topography, climate, and vegetation. The 13 samples collected outside of mapped seed zones were placed into the category of 'outside'. We aggregated lithology types from the

State Geological Map Compilation database (Horton et al. 2017) to five groups. We determined whether a sample was collected east or west of the Continental Divide by using spatial analyses on a geodatabase feature class of sample locations and a shapefile of the Continental Divide (U.S. Geological Survey 2002). We initially performed analyses using actual elevation and using equivalent elevation, which accounts for the latitudinal range of our study area (Windmuller-Campione and Long 2016), but we report only results based on actual elevation due to lack of significant differences between the two metrics.

To identify important predictors of identification accuracy, we developed a random forests model in R package randomForests (R Core Team 2016) using a classification threshold of 0.5 (James et al. 2013), with 500 trees for evaluation (parameter ntree = 500 and mtry = 3). We used 10-fold cross-validation to evaluate model performance. We chose random forests because it provides intuitive interpretation of variable importance, is robust to collinearity and interaction among predictor variables, and makes no a priori assumptions about the distributions of response or predictor variables (Cutler et al. 2007). Significant predictors were identified by their corresponding decrease in random forests model accuracy (i.e., not identification accuracy) and Gini index (Cutler et al. 2007; James et al. 2013). Mean decrease in accuracy measures the contribution of each variable to the overall accuracy of the model, whereas Gini index is a measure of node purity (i.e., how accurate is each decision point, or node) within the classification tree (James et al. 2013). The Gini index method of calculating variable importance results in a strong preference for continuous variables or those with many categories (Strobl et al. 2007).

To complement modelling, we examined the relationship between predictor variables and identification accuracy. We compared field- versus lab-identified whitebark pine presence across different predictor variable values or categories to better understand the circumstances in which misidentification is most likely to occur. Wilcoxon rank sum tests (for continuous predictor variables) and chi-square tests of association (for categorical predictor variables) were performed to test for significant associations between identification accuracy and the predictor variables (Zar 1996) (critical p-value =

0.05 for each method). We calculated Cramer's V scores to determine the strength of association with each categorical predictor variable. Cramer's V scores quantify the strength of the association among two categorical variables, which in our analysis were done via chi-square tests, where the values of V range from zero (no association) to one (perfect association) (Cohen 1988). Values less than or equal to 0.3 indicate a weak association, those between 0.4 and 0.5 a medium association, and those greater than 0.5 a strong association. To better understand effects of crew experience, we compared cumulative accuracy for the field crew leader collecting a given sample to that crew leader's experience as of that date. Cumulative accuracy was calculated as mean accuracy of all samples across all plots that a crew leader had collected up to and including each sampling date.

RESULTS:

Field identification accuracy

Genetic analyses of the 295 needle samples collected within the study area revealed that 218 samples came from whitebark pines, and 77 samples came from limber pines. Overall, field identification accuracy was 83% (Table S1 provides details for each misidentified sample). Greater than 99% of samples identified as whitebark pine by field crews were genetically confirmed as whitebark pine. The primary source of error was misidentification of whitebark pines as limber pines, indicated by the 40% false positive rate for limber pine (Table 2), which meant that field crews detected 77% of sampled trees genetically verified as whitebark pines. In contrast, only a single limber pine was misidentified as a whitebark pine. Although identification accuracy was similar for large trees (89%) and saplings (88%), it was notably lower for seedlings (78%). More than half of seedlings identified as limber pine by field crews were whitebark pine, and only 73% of whitebark pine seedlings were correctly identified (Table 2).

Predictors of identification accuracy

Our random forests model correctly classified 88% of observations, based on the predictors in Table 1, and had a Cohen's Kappa value of 0.53 which is generally considered to indicate 'moderate'

agreement between actual and predicted values (Cohen 1988). The two indices used to evaluate relative variable importance (mean decrease in accuracy and Gini index) produced different results. Both metrics indicated that crew leader experience had the most impact on identification accuracy. However, large limber pine trees recorded by field crews on the plot and large whitebark pine trees recorded by field crews on the plot had the second and third largest variable importance scores based on mean decrease in accuracy. Elevation and Julian day had the second and third largest variable importance scores based on the mean decrease in Gini index (Figure 2a). The method of calculating variable importance for Gini index likely contributed to the increased relative importance of the three continuous variables (see 'Methods' for details).

The results of chi-square tests of association (Table 3) and Wilcoxon Rank Sum tests detected significant relationships between identification accuracy and several variables also identified as important by the random forests model (see Table 1 for predictor variable descriptions). For categorical variables, significant associations with identification accuracy were detected for large whitebark pine trees recorded by field crews on the plot, large limber pine trees recorded by field crews on the plot, lithology type, seed zone, forest type group, and size class. Cramer's V scores were highest for large whitebark pines recorded by field crews on the plot (0.346) and large limber pines recorded by field crews on the plot (0.262), suggesting moderate and weak associations, respectively, with identification accuracy. Despite its moderate importance in the random forests model, habitat type was not significantly associated with identification accuracy according to the chi-square test of association. Among our continuous predictors, Wilcoxon Rank Sum tests indicated that only crew leader experience had a significant effect on identification accuracy ($p < 0.001$).

Patterns in misidentification

We quantified the likelihood of misidentification with respect to three types of variables: observer-related, tree-level, and site-level variables. Analysis of observer-related variables indicated that

the experience level of the crew leader was an important predictor of identification accuracy. For correctly identified samples, crew leaders had completed an average of 49 whitebark/limber pine plots in the study area, whereas for incorrectly identified samples, crew leaders had completed an average of 26 plots ($p < 0.001$, Welch's t-test). Our ability to test whether accuracy increased as individual crew leaders gained experience was limited by low sample sizes from many crew leaders (81% of crew leaders collected samples from less than 10 plots). However, a broad range of experience across all crew leaders revealed a strong correlation ($p < 0.001$, Spearman rank correlation) between crew leader experience and cumulative accuracy, both among crew leaders and even for some individuals as their experience increased (Figure 3). Crew leaders who had measured fewer than 25 plots had highly variable cumulative accuracy (56% correct $\pm$ 50% SD), while more experienced crew leaders were more consistently accurate (91% correct $\pm$ 29% SD). In contrast to crew leader experience, the other observer-related variable, 'tally' versus 'non-tally,' had no significant effect on identification accuracy. This indicates that even though some samples were collected from trees that were not included in the FIA dataset, the accuracy rates and trends were still representative of FIA data.

We assessed how cone presence influenced identification accuracy using two tree-level variables associated with the likelihood of cone presence: tree size class and Julian day. To accomplish this, we compared accuracy rates among size classes and tested for relationships between accuracy and Julian day. The clear differences in accuracy among samples collected from seedlings versus from large trees and saplings in our confusion matrices (Table 2) were not supported by the low relative importance of 'Size_Class' in the random forests model (Figure 2) and low Cramer's V score (0.176) in the chi-square test (Table 3). This may be due to similar accuracies for large trees and saplings, which likely dampened the effect of seedlings. Julian day, which is an indicator of cone phenology and development, was one of the most important predictors of identification accuracy in the random forests model. A partial dependence plot of Julian day versus identification accuracy revealed that the likelihood of correct

identification was relatively low prior to mid-July, reached a peak from mid-August through late-September, and then declined (Figure 2b).

The most important site-level predictors of identification accuracy were whether large trees of either species ('PIAL_Trees') or ('PIFL_Trees') were recorded by field crews on the plot, as confirmed by the results of the random forests model (Figure 2), chi-square tests of association (Table 3), and comparison of field-identified versus lab-identified species frequencies (Table 3). We found substantially higher identification accuracy for samples (regardless of tree size) collected from plots where the large trees were recorded as whitebark pine (> 99% accurate), compared to those where they were recorded as limber pine (66% accurate). In addition, all 56 plots where field crews recorded large whitebark pine trees did actually contain lab-identified whitebark pine, while only 32 of 43 plots where field crews recorded large limber pine trees actually contained lab-identified limber pine.

We detected associations between identification accuracy and several other site-level variables, although these were weaker than those for field-identified presence of large whitebark and limber pines. Identification accuracy rates varied widely between seed zones, from 91% accuracy in the Inland Northwest (INLA) seed zone to 72% in the Greater Yellowstone – Grand Teton (GYGT) zone (Table 3). Lower identification accuracy within the GYGT seed zone is also associated with sample collection by crew leaders who were less experienced in measuring whitebark and limber pine (Figure 3).

Identification accuracy was highest in the whitebark pine and limber pine forest type groups (Table 3). Samples from whitebark pine forest types were dominated by whitebark pine (96% of samples lab-identified as whitebark pine) and contained just one misidentification. Similarly, samples from limber pine forest types were dominated by limber pine (93% of samples lab-identified as limber pine), and also contained just one misidentification. The forest type groups with the highest rates of misidentification were the lodgepole pine and the fir/spruce/mountain hemlock (Table 3).

Among habitat type groups, the whitebark pine-timberline and limber pine habitat series had the highest accuracy rates (96% and 88%, respectively), exhibiting a pattern similar to the whitebark pine and limber pine forest type groups. Identification accuracy was lowest (79%) in the subalpine fir series, with a large discrepancy between percent of samples that were lab-identified (98%) versus field-identified (77%) whitebark pine. We detected a strong positive association between whitebark pine occurrence and the presence of subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.); whitebark pine was associated with both the subalpine fir habitat type series (98% of samples lab-identified whitebark pine) and the whitebark pine-timberline series (96% of samples lab-identified whitebark pine), which includes several habitat types that typically contain a subalpine fir component (Pfister et al. 1977). This association is congruous with our finding of high whitebark pine occurrence in the fir/spruce/mountain hemlock forest type; all sites with fir/spruce/mountain hemlock forest types had either subalpine fir or whitebark pine-timberline habitat types.

Misidentifications were concentrated where elevational overlap was greatest between the species: 63% of misidentifications were detected between 2,100 m and 2,500 m, despite only 41% of samples coming from this elevation range (Figure 4). The concentration of misidentifications in this range resulted in a significantly higher mean elevation for field-identified limber pine samples (2,134 m) than that of lab-identified limber pine samples (1,973 m) ($p = 0.013$, Welch's t-test). The field-identified elevation range of whitebark pine was not significantly different than the lab-identified range ($p = 0.49$, Welch's t-test), but the shift in limber pine elevation suggests there is more elevational distinction between the species than was reflected in previously collected FIA data. We also observed that misidentification was most prevalent on plots just below 2,500 m (~8,200 ft) (Figure 4 and Figure 2d partial dependence plot), although only 7 samples were lab-identified as limber pine above 2,500 m.

We detected a weak association (Cramer's $V = 0.210$) between identification accuracy and lithology type (Table 3). We found that identification was 100% accurate within the carbonate

sedimentary lithology type and 44% of samples were lab-identified whitebark pine. However, analysis of identification accuracy among lithology types proved problematic due to the coarse scale of the lithology data (1:1,000,000).

We also found that co-occurrence of whitebark and limber pines on the same plot was more common than was recorded by field crews; Of the 79 plots that had more than one sample collected, eight plots had both whitebark and limber pine genetically identified (~10%), whereas field crews did not correctly identify that there were two species present on any plots. Because field crews did not detect more than one species per plot, identification errors occurred on all eight plots where co-occurrence was lab-identified.

DISCUSSION:

We found that trees identified as whitebark pine in the field were correctly identified more frequently than trees that were field-identified as limber pine. This strong error directionality may be due, in part, to the rapid deconstruction of whitebark pine seed cones for seed removal by dispersers (McCaughey and Schmidt 1990). Whitebark pine seed cones mature between mid-August and mid-September, after which they rapidly disintegrate as the seeds are harvested by Clark's nutcrackers and other agents, leaving small remnants or no evidence of cones (Arno and Hoff 1989; McCaughey and Tomback 2001). In contrast, limber pine seed cones often remain present and intact (Tomback et al. 2011). When the two species co-occur, crews are more likely to see evidence of limber pine and may be more likely to assign that identification to all high-elevation five needle pines in the area. Additionally, post-predation cone remnants on whitebark pine can be mistaken for persistent limber pine cones and lead to misidentification, even in stands that contain only whitebark pine. In addition to contributing to error directionality, cone phenology provides a potential explanation for the relationship of Julian day and identification accuracy (Figure 2b); higher identification accuracy coincides with the time when mature pollen and seed cones are most likely to be present for whitebark pine. An alternative

356 explanation of the Julian day relationship to identification accuracy is that field crews typically sample
357 their highest elevation plots in August and September, and these plots are more likely to be dominated
358 by whitebark pine (Figure 4); 80% of samples collected from mid-July to late-September were lab-
359 identified whitebark pine, versus 55% and 57% before and after this period, respectively.

360 Our results support our expectation that identification errors would be more prevalent for
361 seedlings compared to saplings and large trees due to the difficulty in distinguishing species if cones are
362 absent. However, differences between the genetic sampling protocol and FIA plot measurements
363 indicate that FIA seedling data may be more accurate than our study suggests, even in the study area
364 (see 'Implications for users of FIA data'). Further, the higher identification accuracy for samples from all
365 size classes in the presence of correctly identified large whitebark pine trees suggests that 1) there is a
366 tendency of crews to assign any five-needle pine regeneration to the same species they recorded in the
367 overstory and 2) higher identification accuracy rates for regeneration on plots with large whitebark pines
368 recorded can be explained by higher identification accuracy rates for large whitebark pines (Table 2).

369 A related finding is that identification accuracy is lower in forest types other than whitebark pine
370 or limber pine types. Two previous studies based on FIA data (Goeking and Izlar 2018; Goeking et al.
371 2019) documented the prevalence of whitebark pine within the fir/spruce/mountain hemlock and
372 lodgepole pine forest type groups and noted particularly high densities of regeneration in stands
373 dominated by lodgepole pine. Our results validate that seedlings identified as whitebark pine were
374 virtually always correct, yet more than half of seedlings identified as limber pine were actually whitebark
375 pine. Thus, although these earlier studies quantified abundant whitebark pine regeneration in multiple
376 forest types, they likely underestimated the prevalence of whitebark pine seedlings.

377 The strong positive association we found between whitebark pine and subalpine fir indicates
378 that, in some regions where the ranges of whitebark and limber pines overlap, the ability of a site to
379 support subalpine fir may serve as a strong predictor of the five-needle pine species present. Pfister et

al. (1977) and Steele et al. (1981) found that limber pine occurrence was restricted to just a few of the driest habitat types capable of supporting subalpine fir in Montana and central Idaho, respectively. However, Steele et al. (1983) found that limber pine occurrence was less restricted within habitat types capable of supporting subalpine fir in eastern Idaho and western Wyoming. These resources indicate that, while the whitebark pine – subalpine fir association may be useful for identification in some regions, it may be less reliable in other areas, particularly in the GYGT seed zone, and this relationship warrants more study.

Higher error rates in the GYGT seed zone, which is known for challenges in five-needle pine species distinction (Greater Yellowstone Whitebark Pine Monitoring Working Group 2011; Hansen et al. 2021), may result from the specific combination of lithologies, habitat types, and forest types found within this seed zone. We found higher representation of some lithology types, habitat type groups, and forest type groups that had lower identification accuracy rates in this seed zone compared to other zones (data not presented). Crew leader experience also had substantial influence on identification accuracy, even though we limited the quantification of crew leader experience to measurements of plots in FIA's annual inventory, and thus potentially excluded experience gained from other field work. We found that crew leaders in the GYGT zone had less experience; thus, experience and seed zone may be confounding factors.

Lithology helps determine moisture and nutrient availability and has been tied to whitebark pine and limber pine occurrence patterns (Weaver and Dale 1974; Hansen-Bristow et al. 1990; Weaver 2001). We predicted identification accuracy might be low within the carbonate sedimentary lithology type because resources used by field crews (e.g., Pfister et al. 1977; Steele et al. 1981) mention an affinity for calcareous (i.e., carbonate) substrates by limber pine and not by whitebark pine, yet comprehensive reviews of species substrate preferences suggest this is true only in specific geographic areas (Hansen-Bristow et al. 1990; Weaver 2001). However, this prediction was not supported by our results; all

samples collected from sedimentary (carbonate) lithology type were accurately identified. Although we found a weak overall association between identification accuracy and lithology type, the possibility that samples were collected from inclusions of different lithology types in the coarser scale lithology polygons make this association questionable. If site-specific lithology data were available for RMRS-FIA plots, this analysis would be more useful.

Though we did not examine co-occurrence as a predictor variable, our results indicate that the potential for identification errors markedly increases on sites where whitebark and limber pines co-occur, as noted by others (Greater Yellowstone Whitebark Pine Monitoring Working Group 2011; Hansen et al. 2021) . Because sample collection was limited to a maximum of four samples of each species per plot, true co-occurrence rates are likely higher than the 10% rate we detected. The likelihood of co-occurrence indicates that definitive identification features (e.g., mature cones) on one tree cannot reliably be used to identify nearby trees. This implication poses additional challenges to field crews tasked with identifying trees of all ages in a fixed area and underscores the importance of providing additional identification tools (i.e. genetic analysis).

Implications for users of FIA data

Genetic analysis of whitebark and limber pine samples revealed misidentification rates that exceed FIA's data quality standards. Although over 99% of samples identified as whitebark pine by field crews were actually whitebark pine, the misidentification of many whitebark pine as limber pine meant that field crews correctly identified large trees, saplings, and seedlings of whitebark and limber pine only 89%, 88%, and 78% of the time, respectively. FIA objectives are to correctly identify species $\geq 95\%$ of the time for large trees and saplings and $\geq 85\%$ for seedlings (USDA 2010). Although these misidentification rates are based on FIA field crew measurements, they are likely indicative of error rates from other field-based identification of whitebark and limber pines by trained monitoring crews.

427 These samples were analyzed opportunistically, relying on a previous sampling strategy designed
428 to compare genetics of all tree species across broad scales; thus, sampling was not specifically intended
429 to distinguish whitebark and limber pines. Because crews did not know these samples would be used to
430 test identification accuracy, the effort devoted to identification of these samples is likely representative
431 of RMRS-FIA identification. The geographic range of the original sampling protocol provided 76
432 whitebark and limber pine samples collected outside of the study area. Genetic analysis verified that
433 field identification was 100% accurate for both species outside the study area, indicating that the
434 implications of identification errors are confined to the area of range overlap.

435 The differences between genetic sample collection protocols and FIA field methods create some
436 challenges for understanding implications for FIA data. Foliage collection was limited to one sample per
437 subplot for each species identified in the field, for a maximum of four samples per species per plot. The
438 sample limit, paired with the common assumption that only one 5-needle pine species was present on a
439 plot, reduced the likelihood of identifying undetected species co-occurrence, including dispersed
440 seedlings of a 5-needle pine species not present in the overstory. Needle collection protocol for this
441 study only called for sampling from seedlings when larger, potentially cone-bearing trees were absent
442 from the subplot or when needles could not be reached on these trees, whereas RMRS-FIA protocol
443 measures seedling species regardless of large tree presence. Field crews typically assume that whitebark
444 and limber pine seedlings match the species of nearby large trees. Our results corroborate this
445 assumption on plots with large whitebark pine, which account for approximately 65% of plots with
446 whitebark or limber pine in the study area. This suggests that large tree presence likely increases
447 accuracy on the majority of FIA plots. Seventy-one percent of plots that have whitebark seedlings in
448 recently published FIA data (2010-2019) also have large trees on plot, whereas only 60% of plots with
449 seedlings collected in this study had large trees present on plot. This indicates that whitebark and limber
450 pine seedling identification is likely somewhat better throughout FIA data than our results suggest, even

within the species' range overlap. However, the 2010-2012 sampling design limits the ability to quantify seedling identification accuracy for these species in the broader sample of FIA data.

Despite sampling limitations, this study does help FIA data users understand whether misidentifications introduce substantial bias to estimates of whitebark and limber pine numbers derived from FIA data. Our results suggest that, within our study area, whitebark pine abundance has been underestimated, while limber pine abundance has been overestimated. If we wish to quantify the impact of this bias, we must make several assumptions. First, we must assume that the selected samples are representative of the overall population of whitebark and limber pines on RMRS-FIA plots within our study area. In our study, this is likely true for large trees and saplings, but not for seedlings, suggesting that our results should not be used to quantify the impact of misidentifications on estimations of seedling numbers. Second, we must assume that misidentification rates are similar between the 2010-2012 study period and other years of data collection.

The sample design only evaluated live trees; therefore, factors related to misidentification cannot directly inform whether bias in species identification would be substantially different for dead trees. However, some information can be inferred based upon the methods of FIA data collection. For example, dead trees in the FIA dataset are either 1) trees that were dead at the time of initial plot establishment or 2) trees that were alive at a previous plot visit and have since died. Patterns of misidentification are likely similar to those of live trees for the latter because the initial identification was made when the tree was alive. Our results provide no evidence that live and dead whitebark pine trees were underestimated at different rates or that previously published estimates of live-to-dead ratios of whitebark pine trees (Goeking and Izlar 2018) are biased.

In addition to affecting estimates of tree numbers, bias resulting from species misidentifications has implications for the use of FIA data in species distribution modelling. Our results indicate that data used to develop species distribution models for whitebark pine on forestland likely include only a few

cases where the trees are actually limber pines. However, these models are likely missing additional locations where whitebark pine was present but was misidentified as limber pine. Further, we found that misidentifications were not evenly distributed with respect to elevation and habitat type series, which are closely correlated with climatic conditions (Pfister et al. 1977; Steele et al. 1981). However, because field- and lab-identified elevation ranges of whitebark pine samples were not significantly different, inferences based on FIA data concerning the elevation distribution of whitebark pine should remain valid. Given that we found that 40% of samples field-identified as limber pine were actually whitebark pine, species distribution modeling of limber pine based on FIA data likely contain more errors of commission (i.e., predicting limber pine presence where it does not occur) in areas of range overlap with whitebark pine. Additionally, significantly higher mean elevation for field-identified limber pine samples than that of lab-identified limber pine samples means that inferences based on FIA data about the elevation distribution of limber pine need to be reevaluated. While some of these results provide assurance of data quality, they also indicate that it is important to implement tools that improve identification accuracy, not only within FIA, but also for any probability-based field studies of these two species in regions of range overlap.

Our results indicate ways the FIA program, and other studies that rely on field-based species identification, can improve identification accuracy. First, sample protocols should prioritize non-cone-bearing trees for genetic analyses that provide definitively accurate identification of these individuals (Alongi et al. 2019; Hansen et al. 2021). The genetic analyses have proven relatively economical; current laboratory costs are about \$20 per sample (with added costs and time for sample collection, cataloging, and shipping). Needle sampling and lab verification could also be applied beyond the zone of overlap to validate these two species' geographic ranges and potentially identify populations outside their currently known range. However, such an objective would require a larger sample size than used in the current study. Second, trends in crew leader experience suggest that training on whitebark pine versus limber

pine identification led by experienced personnel could increase accuracy when cones are absent and genetic analyses is not possible, such as when a tree is dead, needles are out of reach, or cost is prohibitive. Suggested training would include how to use important site-level predictor variables such as forest type and habitat type and would emphasize that species identification should be made at the tree versus stand level, since co-occurrence is more likely than expected.

These two approaches for improving quality complement each other; as the data from genetic identification efforts provide a more comprehensive accounting of error and species occurrence patterns, training materials can be improved. Our results indicate that improved training may increase future data quality, even in studies which may not have the means for genetic identification. Based on these results, in 2022 RMRS-FIA implemented a protocol that aims to genetically identify all non-cone bearing large trees, all saplings, and up to 5 seedlings per subplot of whitebark and limber pine. Improved data quality is important not only for FIA and other field-based monitoring programs, but also for improved accuracy of models and maps of seedling niches and climate change projections, all of which rely on field-based observations for calibration and validation.

Conclusions:

Identification accuracy of whitebark and limber pines by RMRS-FIA field crews fell below FIA's data quality standards for all tree size classes in our study area. With respect to whitebark pine, field crew identifications showed high specificity (< 1% of limber pines were field-identified as whitebark pines) but relatively low sensitivity (about 25% of whitebark pines were not field-identified as such). This resulted in underestimation of whitebark pine abundance and overestimation of limber pine abundance. Species distribution modelling efforts calibrated with FIA data will include very few false presences of whitebark pine, although some sites with whitebark pine present will be omitted from calibration datasets. In contrast, species distribution models for limber pine will be influenced by a greater number of false positives that could negatively affect model accuracy.

523 Misidentifications were confined to regions of range overlap, implying that potential biases were
524 limited to those geographic areas. Within regions of range overlap, sampling limitations make it difficult
525 to quantify the true impact of biases on estimates of whitebark and limber pine numbers as well as
526 ratios of dead to live trees. Despite sampling limitations, we found that co-occurrence of whitebark and
527 limber pines was more common than recorded by field crews and that seedling identification was
528 particularly challenging. Better understanding of patterns of misidentification gained through this study
529 has helped us develop a path toward improvement that focuses on needle collection from non-cone
530 bearing trees by crews that are trained to use multiple factors for species identification.

Table titles and figure captions:

Table 1. Summary of predictor variables as potential determinants of field identification accuracy.

Table 2. Species identification accuracy metrics. PIAL = whitebark pine; PIFL = limber pine.

Table 3. Whitebark and limber pine identification across nine categorical predictor variables. Predictors with significant associations with identification accuracy according to chi-square contingency tests have Cramer's V scores in bold (critical p-value = 0.05). Larger values of Cramer's V indicate stronger association.

Figure 1. Map of study location and whitebark and limber pine in the Rocky Mountain Research Station-Forest Inventory and Analysis (RMRS-FIA) states*. Symbology for plot locations inside the study area (a) indicates the species present and accuracy of identification(s) (ID) on each plot. Samples from outside the study area were all correctly field-identified in agreement with the species range maps. The buffered ranges of whitebark pine (b) and limber pine (c) are based FIA records of whitebark and limber pine and range maps from Whitebark Pine Ecosystem Foundation (2014 and 2019) and USDA Forest Service, Forest Health Protection (Forest Health Technology Enterprise Team 2023). *RMRS-FIA states: Arizona, Colorado, Idaho, Montana, Nevada, New Mexico, Utah, and Wyoming.

Figure 1 alt text: Maps of the study area labeled a-c: 1a) A map of Colorado, Idaho, Montana, Nevada, Utah, and Wyoming with the outlined study area, range maps for whitebark and limber pine, and needle sample collection locations. 1b and 1c) Maps of all Rocky Mountain states with points for all FIA plots that had field-identified whitebark pine (1b) and limber pine (1c) and the 35-kilometer buffered range of each respective species.

Figure 2. Results of random forests classifications used to predict identification accuracy. The variable importance plots (a) present the relative importance of each variable in predicting if a sample was correctly or incorrectly identified. Variables are listed in order of relative importance from top to bottom, with higher mean decrease accuracy and mean decrease Gini values corresponding to greater variable

importance. Panels b-f are partial dependence plots providing a graphical depiction of the marginal effect of a given variable on the likelihood of correct identification across different predictor variable values. The y-axis values are similar to a logit scale, with higher values indicating a higher likelihood of correct identification (see Cutler et al. 2007, Appendix C). Variables are described in Table 1.

Figure 2 alt text: Graphical outputs from random forests modeling, labeled a-f: 2a) A pair of plots showing the relative importance values of nine predictor variables (y-axes) in relation to mean decrease in accuracy (left) and Gini coefficient (right) (x-axes). 2b-f) Plots depicting the marginal effects of the most important predictor variables on the likelihood of correct identification: Julian day (2b), crew leader experience (2c), elevation (2d), field recorded presence or absence of large whitebark pine trees on plot (2e), and field recorded presence or absence of large limber pine trees on plot (2f).

Figure 3. Crew leader experience and cumulative accuracy across seed zones. Cumulative accuracy increases and becomes less variable for crew leaders with more experience (a). Crew leaders typically work within a specific geographic area; the distribution of experience across seed zones of sample collection (b) illustrates how geographic location and associated variables interact with trends in crew leader accuracy.

Figure 3 alt text: Graphs of crew leader experience labeled a-b: 3a) A scatter plot with a trendline that shows cumulative accuracy (y-axis) related to crew lead experience (x-axis). The color and symbol of each point represents the seed zone and crew leader identity, respectively, of each sample collection. 3b) Box plots show the distribution of crew leader experience in each seed zone.

Figure 4. Elevational distribution of whitebark and limber pine needle samples (n = 295). Stacked bars show the elevational distribution of correct and incorrectly identified samples for each species (a). Lab-identified limber pine (*Pinus flexilis*) is displayed in green, and lab-identified whitebark pine (*Pinus albicaulis*) is displayed in purple. Darker shading of each color indicates samples that were correctly field-identified, and lighter shading indicates incorrect field-identification. The effects of identification error

579 on elevation distribution are illustrated by a comparison of box plots of elevation range based on lab-
580 identified versus field-identified whitebark pine (b) and limber pine (c).

581 **Figure 4 alt text:** Graphs of field- and lab-identified elevation, labeled a-c: 4a) Stacked bars show the
582 number of samples collected (y-axis) across elevation range (x-axis). 4b and 4c) Box plots show the
583 elevation distribution of samples lab-identified and field-identified as whitebark pine (4b) and limber
584 pine (4c).

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790 **Supplementary materials description:**

791 Table S1: Selected attributes for each sample that was incorrectly identified in the field.

Table 1. Summary of predictor variables as potential determinants of field identification accuracy.

Table 1. Summary of predictor variables as potential determinants of field identification accuracy.

Predictor class	Predictor description	Code	Prediction tested	Source	Type
Observer-related	crew leader experience	Crew_Lead_Experience	ID accuracy is affected by experience in distinguishing five-needle pines	Derived from FIA data ¹	continuous
	‘tally’ versus ‘non-tally’ sample	Tally	ID accuracy is affected by whether additional data is collected on the sampled tree	Field sample labels	categorical
Tree-level	size class (large tree, sapling, seedling, unknown)	Size_Class	The presence of reliable ID characteristics such as cones varies by size class	Field sample labels	categorical
	Julian day sample collected	Julian_Day	Phenology and cone development influence ID accuracy	Calculated from FIA data	continuous
Site-level	actual elevation (m)	Elevation_Actual	Species occurrence varies with actual elevation, influencing ID accuracy	FIA data (ELEV)	continuous
	habitat type series	Habitat_Type	Species occurrence varies by habitat type, influencing ID accuracy	FIA data (HABTYPCD1)	categorical
	forest type (field designation)	Forest_Type	Species occurrence varies by forest type, influencing ID accuracy	FIA data (FLDTYPCD)	categorical
	whitebark pine seed zone	Seed_Zone	Species occurrence varies by seed zone, influencing ID accuracy	Mahalovich and Hipkins	categorical
	lithology type	Lithology	ID accuracy is affected by assumptions made about species/substrate relationships	SGMC ²	categorical
	large whitebark pine trees recorded (≥12.7cm diameter)	PIAL_Trees	ID accuracy of immature trees is affected by large PIAL trees recorded on the plot	Derived from FIA data ³	categorical
	large limber pines trees recorded (≥12.7cm diameter)	PIFL_Trees	ID accuracy of immature trees is affected by large PIFL trees recorded on the plot	Derived from FIA data ³	categorical
	East/West of Continental Divide	East_West_CD	Species occurrence varies by location east or west of the divide, influencing ID accuracy	Derived from FIA data	categorical

¹Determined for each sample by counting the number of FIA plots in the study area with whitebark pine and/or limber pine present that a crew leader had measured at the time of sample collection.

²State Geological Map Compilation database

³Determined from data entered by field crews (field-identified) and not from genetic (lab-identified) verifications. As such, these variables suggest whether the field crew believed that large trees of whitebark or limber pine were present on the plot, not whether they were genetically confirmed.

Table 2. Species identification accuracy metrics.

Table 2. Species identification accuracy metrics. PIAL = whitebark pine; PIFL = limber pine.

Tree size class	Number of samples	Proportion correctly identified	PIAL false positive	PIFL false positive	PIAL sensitivity/ PIFL specificity	PIFL sensitivity/ PIAL specificity
All samples	295	0.83	0.01	0.40	0.77	0.99
Seedlings only	103	0.78	0.00	0.56	0.73	1.00
Saplings only	43	0.88	0.00	0.22	0.80	1.00
Large trees only (≥12.7 cm dbh)	115	0.89	0.00	0.30	0.85	1.00
Unknown size only	34	0.71	0.06	0.50	0.62	0.90

Table 3. Whitebark and limber pine identification across nine categorical predictor variables.

Table 3. Whitebark and limber pine identification across nine categorical predictor variables. Predictors that are significantly associated with identification accuracy, as determined by chi-square contingency tests, have Cramer's V scores in bold (critical p-value = 0.05). Larger values of Cramer's V indicate stronger association.

Code	Category	Percent of samples identified as whitebark pine		Sample count	Percent of correctly identified samples	Cramer's V of identification accuracy
		FIELD	LAB			
Tally	YES	62	77	181	85	0.070
	NO	49	68	114	79	
Size_Class	Seedling	60	83	103	78	0.176³
	Sapling	47	58	43	88	
	Tree	62	73	115	89	
	Unknown	47	71	34	71	
Habitat_Type ¹	ABLA	77	98	173	79	0.145 ⁴
	PIAL-Timberline	100	96	25	96	
	PIFL	0	10	39	90	
	PSME	12	31	49	82	
	Other	56	67	9	89	
Forest_Type	Douglas-fir Group	33	48	69	86	0.194⁴
	Fir/Spruce/Mountain Hemlock Group	77	97	71	80	
	Limber Pine Group	0	7	15	93	
	Lodgepole Pine Group	71	97	89	74	
	Whitebark Pine Group	100	96	24	96	
	Other forest type groups	15	22	27	93	
Seed_Zone ²	BTIP	74	89	57	84	0.207⁴
	CLMT	54	65	92	89	
	GYGT	50	76	101	72	
	INLA	75	84	32	91	
	Outside	15	23	13	92	
Lithology	Igneous	79	95	82	84	0.210⁴
	Metamorphic	65	83	89	82	
	Sedimentary (carbonate)	44	44	16	100	
	Sedimentary (other)	34	46	83	86	
	Unconsolidated	44	84	25	60	
PIAL_Trees	Present	100	99	118	99	0.346
	Absent	29	57	177	72	
PIFL_Trees	Present	0	34	83	66	0.262
	Absent	80	90	212	89	
East_West_CD	East	48	63	179	84	0.027
	West	72	91	116	81	

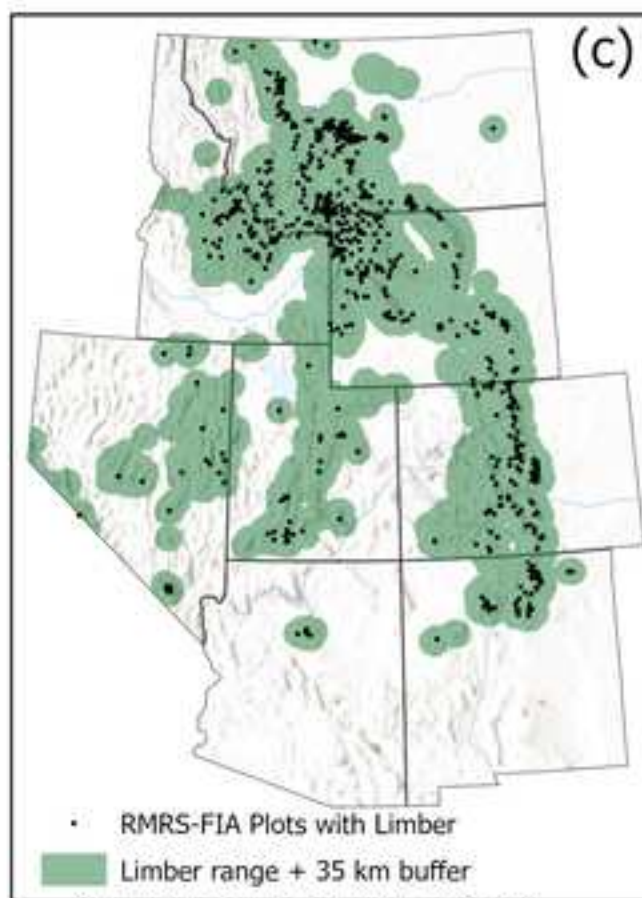
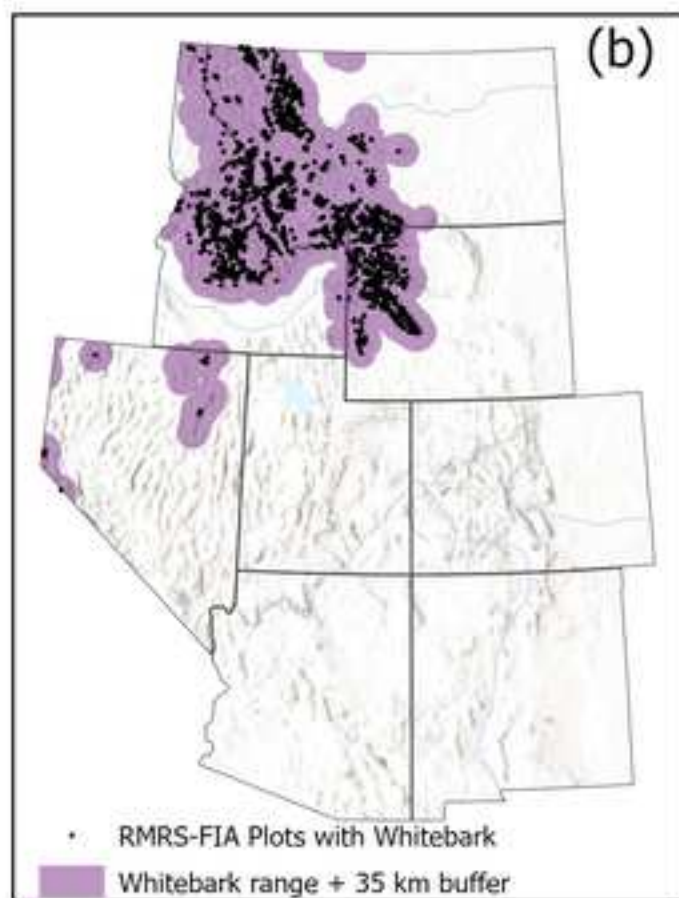
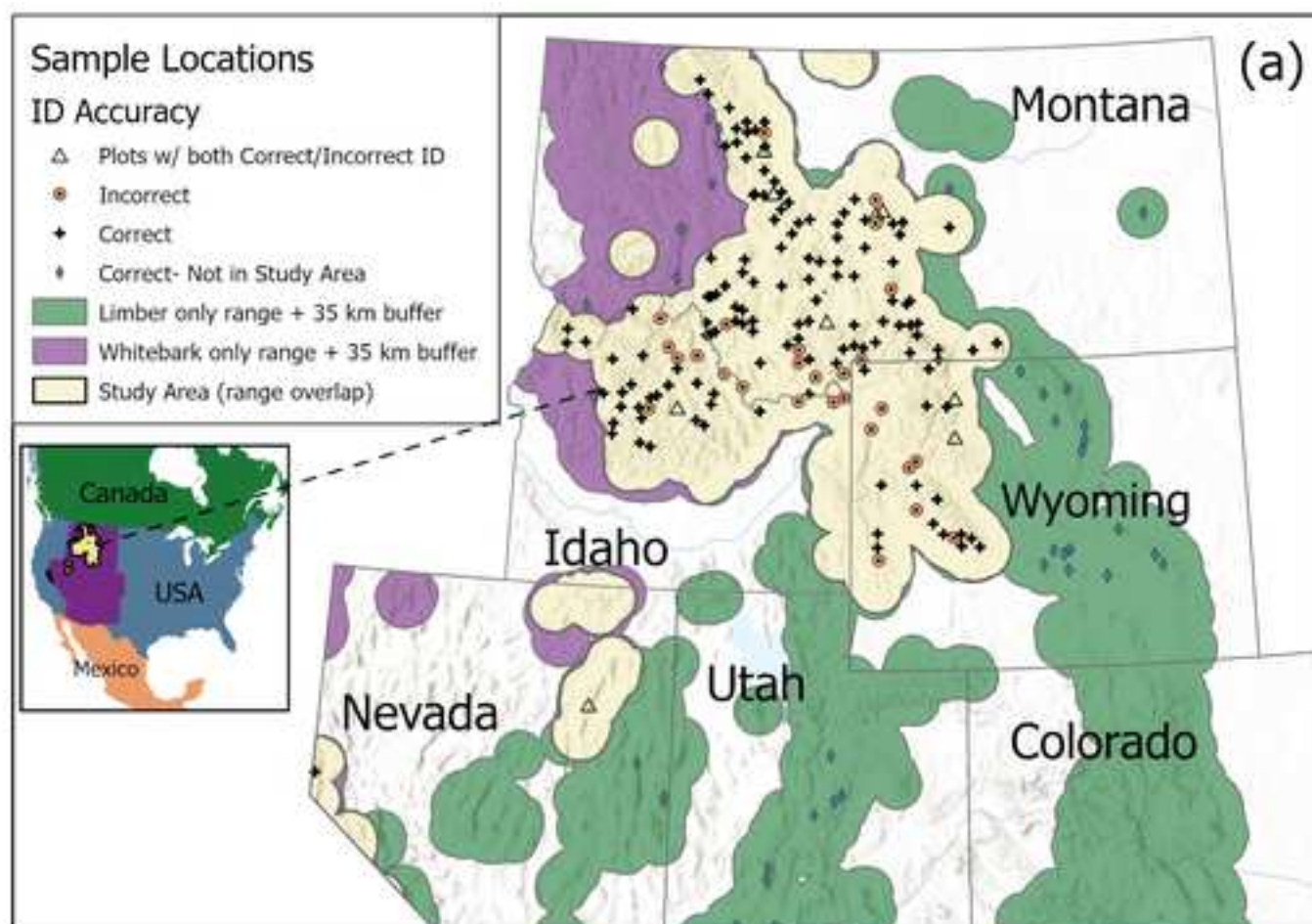
¹ABLA = *Abies lasiocarpa* series, PIAL-TIMBERLINE = *Pinus albicaulis* and timberline habitat types, PIFL = *Pinus flexilis* series, PSME = *Pseudotsuga* series, Other = other habitat types

²Whitebark pine seed zones from Mahalovich and Hipkins (2011): BTIP = Bitterroots – Idaho Plateau, CLMT = Central Montana, GYGT = Greater Yellowstone – Grand Teton, INLA = Inland Northwest, Outside = Nevada seed zone or outside any of the seed zones

³Not significant if UNKNOWN category is excluded

⁴25% or more of cells have expected counts < 5.

Figure 1. Map of study location and whitebark and limber pine in the Rocky Mountain Research Station-Forest Inventory and



ESRI, HERE, Garmin, FAO, NOAA, USGS, EPA

Figure 2 Results of random forests classifications used to predict identification accuracy

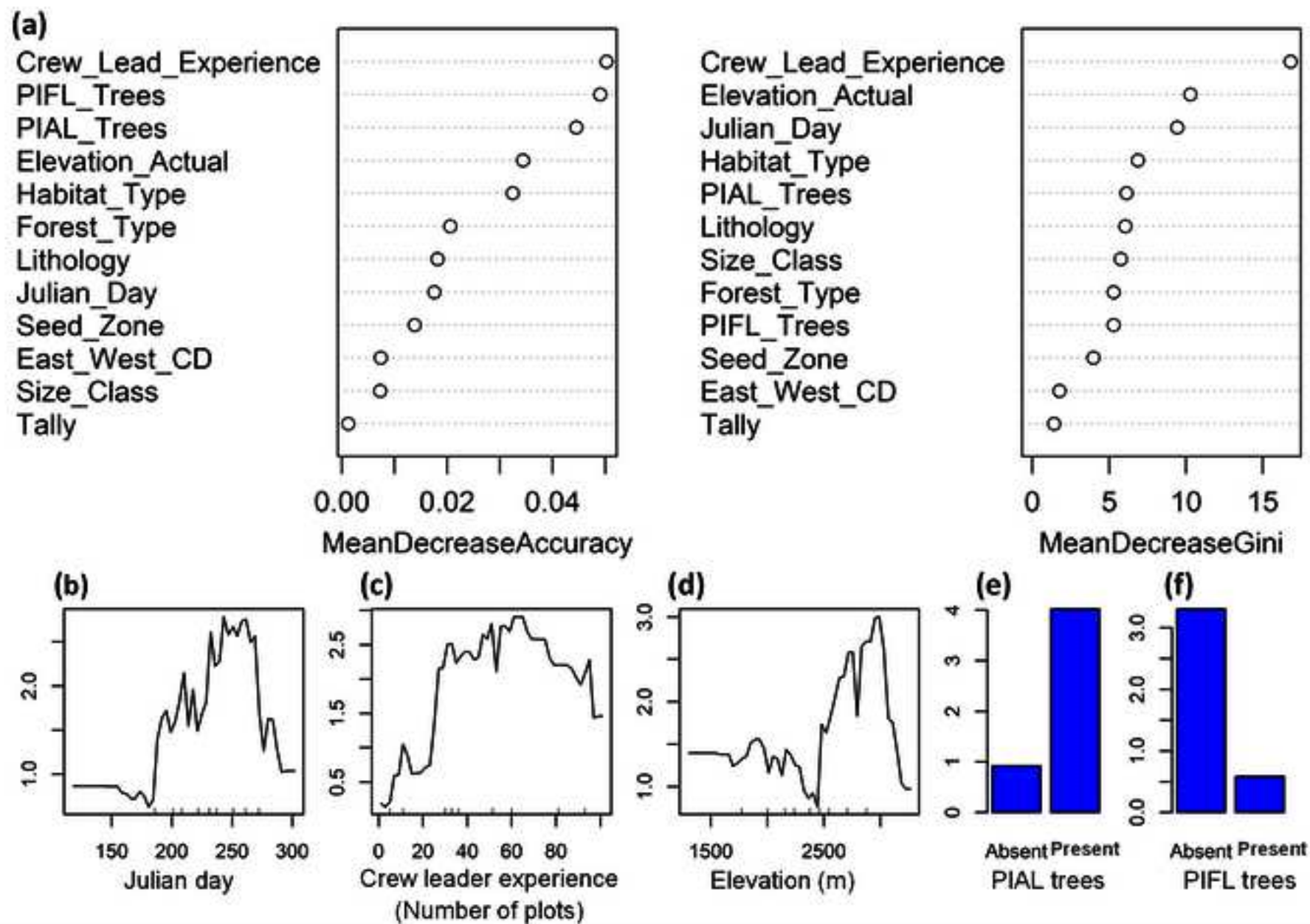


Figure 3 Crew leader experience and cumulative accuracy across seed zones

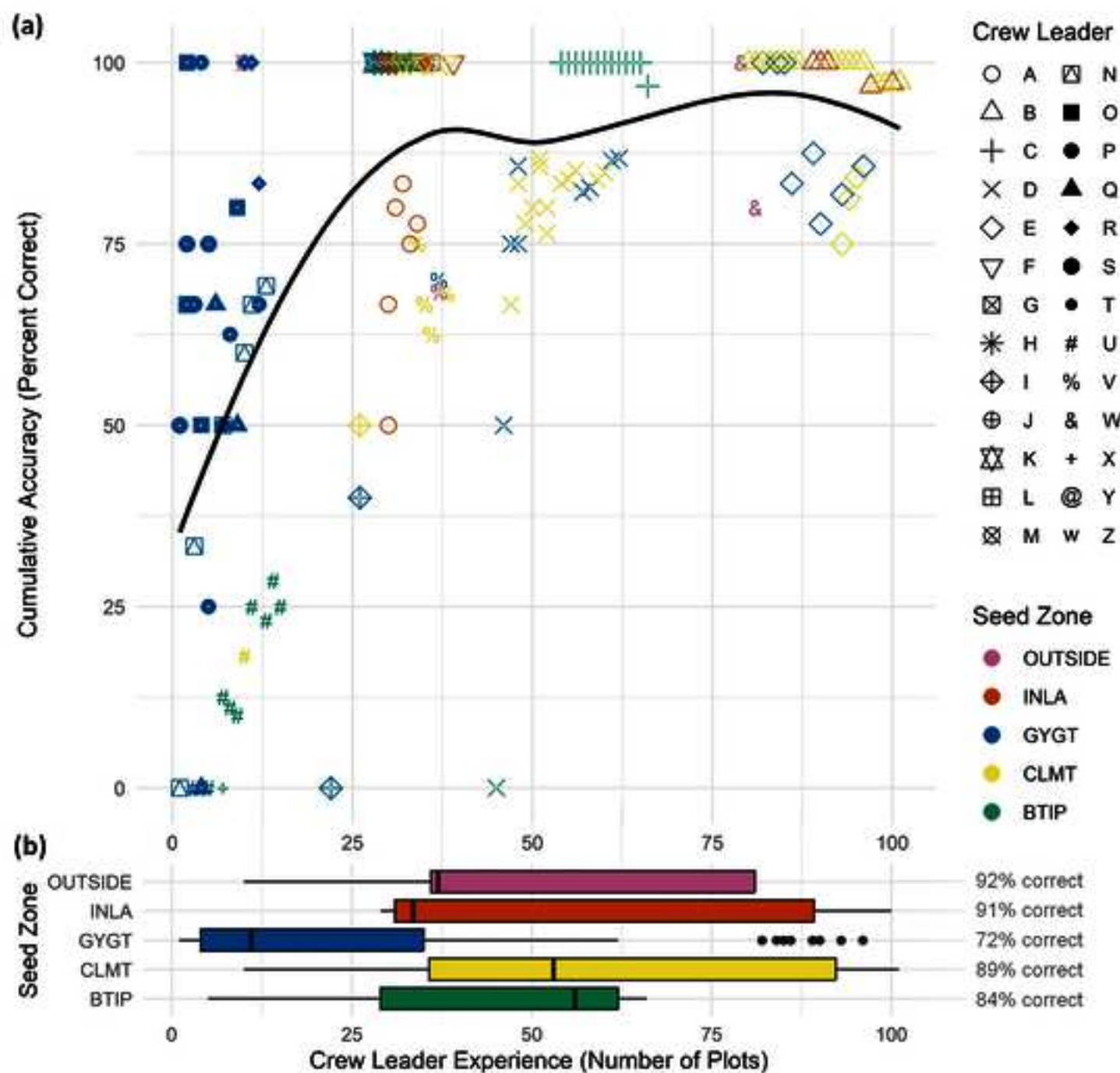


Figure 4 Elevational distribution of whitebark and limber pine needle samples

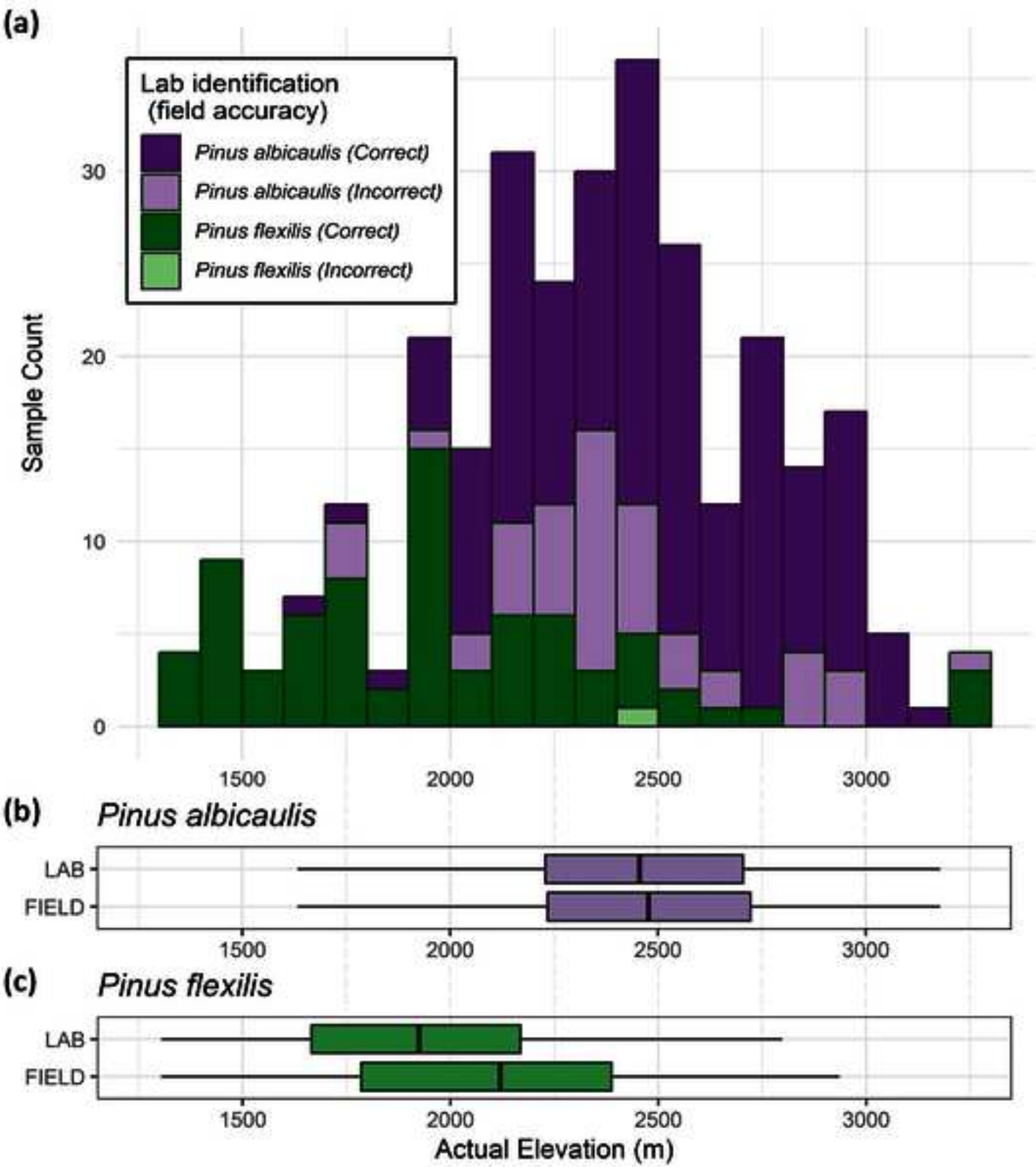


Table S1. Selected attributes for each sample that was incorrectly identified in the field.												
Number of samples collected on plot ¹	Size class of sampled tree	Species ² (lab-identified)	Elevation in meters (approx ³)	Julian day of sample collection	Crew leader ⁴	Crew leader experience ⁵	Number of Five-Needle Pines Recorded on the Plot					
							<i>Pinus albicaulis</i>			<i>Pinus flexilis</i>		
							Large trees	Saplings	Seedlings	Large trees	Saplings	Seedlings
<u>2</u>	Sapling	PIAL	2655	265	C	66	0	0	2	1	0	2
1	Sapling	PIAL	2307	180	X	7	0	0	0	0	0	0
<u>2</u>	Sapling	PIAL	2195	251	V	38	0	0	0	2	0	0
<u>3</u>	Sapling	PIAL	2387	221	V	35	0	0	0	3	3	9
1	Sapling	PIAL	2454	224	N	1	0	0	0	0	1	5
4	Seedling	PIAL	2396	181	U	4	0	0	0	0	0	10
4	Seedling	PIAL	2396	181	U	4	0	0	0	0	0	10
4	Seedling	PIAL	2396	181	U	4	0	0	0	0	0	10
4	Seedling	PIAL	2396	181	U	4	0	0	0	0	0	10
1	Seedling	PIAL	1795	264	U	13	0	0	0	0	0	1
1	Seedling	PIAL	2548	185	U	5	0	0	0	0	0	5
1	Seedling	PIAL	2365	221	U	9	0	0	0	0	0	3
1	Seedling	PIAL	2597	215	U	8	0	0	0	2	0	3
2	Seedling	PIAL	2268	222	D	52	0	0	0	1	0	0
1	Seedling	PIAL	2402	223	V	36	0	0	0	0	0	0
<u>3</u>	Seedling	PIAL	2259	272	B	97	0	0	0	3	0	1
<u>4</u>	Seedling	PIAL	2128	278	Z	4	0	0	0	1	1	0
3	Seedling	PIAL	2335	181	I	22	0	0	0	0	0	6
3	Seedling	PIAL	2335	181	I	22	0	0	0	0	0	6
1	Seedling	PIAL	2158	260	E	93	0	0	0	0	0	0
1	Seedling	PIAL	2801	251	Q	0	0	0	0	0	0	11
3	Seedling	PIAL	2786	240	P	25	0	0	0	1	0	5
3	Seedling	PIAL	2786	240	P	25	0	0	0	1	0	5
3	Seedling	PIAL	2786	240	P	25	0	0	0	1	0	5
1	Seedling	PIAL	2536	278	R	12	0	0	0	1	0	1
3	Seedling	PIAL	2914	234	N	3	0	0	0	2	0	8
3	Seedling	PIAL	2914	234	N	3	0	0	0	2	0	8

1	Seedling	PIAL	2118	242	O	4	0	1	6	0	2	10
2	Large tree	PIAL	2347	290	U	15	0	0	0	3	1	0
2	Large tree	PIAL	2347	290	U	15	0	0	0	3	1	0
2	Large tree	PIAL	2268	222	D	52	0	0	0	1	0	0
1	Large tree	PIAL	2460	209	E	86	0	0	0	2	0	0
3	Large tree	PIAL	2256	202	V	34	0	0	0	9	0	5
3	Large tree	PIAL	2256	202	V	34	0	0	0	9	0	5
3	Large tree	PIAL	2256	202	V	34	0	0	0	9	0	5
<u>3</u>	Large tree	PIAL	2387	221	V	35	0	0	0	3	3	9
<u>4</u>	Large tree	PIAL	2128	278	Z	4	0	0	0	1	1	0
1	Large tree	PIAL	2134	201	D	48	0	0	0	1	0	0
<u>4</u>	Large tree	PIAL	2975	247	W	80	0	0	0	26	4	0
3	Large tree	PIAL	2914	234	N	3	0	0	0	2	0	8
1	Large tree	PIAL	2390	267	Q	9	0	0	0	2	1	10
1	Unknown	PIAL	2079	166	U	3	0	0	0	0	0	0
1	Unknown	PIAL	1939	167	U	3	0	0	0	0	0	0
1	Unknown	PIAL	2524	182	D	45	0	0	0	0	0	0
1	Unknown	PIAL	2237	256	D	57	0	0	0	1	0	0
3	Unknown	PIAL	2335	181	I	22	0	0	0	0	0	6
1	Unknown	PIAL	2390	236	E	90	0	0	0	0	0	1
1	Unknown	PIAL	1783	190	A	50	0	0	0	0	0	1
2	Unknown	PIAL	2076	236	A	75	0	0	0	0	0	0
<u>2</u>	Unknown	PIAL	1896	220	S	1	0	0	0	0	1	0
<u>2</u>	Unknown	PIFL	2518	228	S	3	3	0	0	0	0	0

¹ Numbers in bold italics with underline indicate samples from plots with lab-identified samples of both species.

² PIAL = *Pinus albicaulis*; PIFL = *Pinus flexilis*

³Our analysis was based on actual plot elevation, which cannot be publicly released. Elevations presented in this table are the publicly available values based on approximate plot coordinates. See Burrill et al. 2023 (Sections 2.4.20 – 2.4.22, SURVEY.RSCD = 22) for more details.

⁴ Unique letter for each crew lead follow those used in Figure 3.

⁵ Crew leader experience is the count of FIA plots in the study area with whitebark pine and/or limber pine present that a crew leader had measured at the time of sample collection (including the plot from which the sample was taken).