

Title: Forest types outpaced tree species in range shifts under global change in the United States and Canada

Authors: Akane O. Abbasi¹, Christopher W. Woodall², Javier G. P. Gamarra³, Cang Hui⁴, Nicolas Picard⁵, Thomas Ochuodho⁶, Sergio de-Miguel^{7,8}, Rajeev Sahay⁹, Songlin Fei¹⁰, Alain Paquette¹¹, Han Y. H. Chen¹², Ann Christine Catlin¹³, Jingjing Liang^{1*}

Affiliations:

1. Forest Advanced Computing and Artificial Intelligence Lab (FACAI), Department of Forestry and Natural Resources, Purdue University; 715 W. State St., West Lafayette, IN 47907, USA.
2. United States Department of Agriculture, Forest Service; 271 Mast Rd., Durham, NH 03824, USA.
3. National Forest Monitoring (NFM) Team, Forestry Division, Food and Agriculture Organization of the United Nations; Viale delle Terme di Caracalla, 00153 Rome, Italy.
4. Department of Mathematical Sciences, Stellenbosch University; Merriman Avenue, Stellenbosch 7602, South Africa.
5. GIP ECOFOR; 42, rue Scheffer, 75116 Paris, France.
6. Department of Forestry and Natural Resources, University of Kentucky; 208A Thomas Poe Cooper Building, Lexington, KY 40546, USA.
7. Department of Crop and Forest Sciences, University of Lleida; Av. Rovira Roure 191, 25198 Lleida, Spain.

- 22 8. Joint Research Unit CTFC – AGROTECNIO – CERCA; Av. Rovira Roure 191, 25198
23 Lleida, Spain.
- 24 9. Department of Electrical and Computer Engineering, University of California San Diego;
25 9500 Gilman Dr., La Jolla, CA 92093, USA.
- 26 10. Department of Forestry and Natural Resources, Purdue University; 715 W. State St.,
27 West Lafayette, IN 47907, USA.
- 28 11. Centre for Forest Research, Université du Québec à Montréal; 141 Président-Kennedy,
29 Montréal, QC, H2X 1Y4, Canada.
- 30 12. Faculty of Natural Resources Management, Lakehead University; 955 Oliver Road,
31 Thunder Bay, ON, P7B 5E1, Canada.
- 32 13. Rosen Center for Advanced Computing, Purdue University; 101 Foundry Dr., West
33 Lafayette, IN 47906, USA.

34 *Correspondence: Jingjing Liang; 715 W. State St., West Lafayette, IN 47907, USA;
35 albeca.liang@gmail.com; 001-765-496-0254
36

37 **Abstract:** Mounting evidence suggests that geographic ranges of tree species worldwide are
38 shifting under global environmental changes. Little is known, however, about if and how these
39 species' range shifts may trigger the range shifts of various types of forests. Markowitz's
40 portfolio theory of investment and its broad application in ecology suggest that the range shift of
41 a forest type could differ substantially from the range shifts of its constituent tree species. Here,
42 we tested this hypothesis using *in situ* forest inventory records of more than 9 million trees from
43 596,282 sample plots located across Alaska, Canada, and the contiguous United States. We
44 systematically compared historical range shifts of 43 classified forest types and the range shifts

of constituent tree species over the past 50 years and found that forest types shifted at $86.5 \text{ km} \cdot \text{decade}^{-1}$ on average, more than three times as fast as the average of constituent tree species ($28.8 \text{ km} \cdot \text{decade}^{-1}$). We showed that a predominantly positive covariance of the species range and the change of species relative abundance triggers this marked difference. Our findings provide an urgently needed scientific basis for a new paradigm of adaptive forest management and conservation in mitigating the impacts of rapid forest transformation under climate change.

Introduction

Trees are immobile organisms, but tree species worldwide are found to undergo substantial changes in geographic distributions under global change. Some tree species move to higher latitudes¹⁻⁴, while some move southward^{3,5}; some move longitudinally⁶, while other species move altitudinally^{7,8}. Little is known, however, about whether and how this substantial shifting and reshuffling of tree species ranges may cause an overall type of forest – a distinctive assemblage of tree species distributed across a wide geographical extent – to shift its range.

Although past research has significantly advanced our understanding of tree species range shifts¹⁻⁸ and patterns of tree fecundity and recruitment⁹, the range shifts of forest types and how they differ from those of tree species remain largely unknown. In forest management and related climate change mitigation practices, forest types are often expected to shift at the same speed as their constituent tree species^{3,4}. However, as exemplified in Markowitz's portfolio theory of investment¹⁰, the change of an ensemble can differ from the changes of its constituents. An ecological hypothesis¹¹⁻¹³, derived from the portfolio theory (hereafter, portfolio hypothesis), postulates that the dynamics of an ecological community are not the same as the dynamics of its constituent species. According to the portfolio hypothesis, the speed and direction of forest-type

range shifts can differ substantially from the average speed and direction of tree species range shifts. However, this hypothesis has never been formulated and tested for forest type dynamics.

Here, we formulated and tested the portfolio hypothesis on the divergent range shift rates between forest types and constituent tree species. To do this, we collated a continental-scale forest inventory database containing more than 596,282 permanent sample plots located across North America. Based on repeated *in situ* measurements of more than 20 million trees in these plots, we classified forested areas across the North American continent into 43 forest types in eight forest biomes and three arch-biomes, using an established classification algorithm (see Fig. 1, Extended Data Table 1, and Supplementary Information for details). We then quantified geographic ranges of forest types and individual tree species, as well as their temporal changes between 1970–1999 and 2000–2019.

Results and Discussion

Forest types outpaced tree species in range shifts

At individual species level, Sitka spruce (*Picea sitchensis*) had the greatest velocity in range shifts ($480.4 \text{ km} \cdot \text{decade}^{-1}$), followed by balsam fir (*Abies balsamea*; $438.6 \text{ km} \cdot \text{decade}^{-1}$) and gray alder (*Alnus incana*; $354.6 \text{ km} \cdot \text{decade}^{-1}$) in terms of the distance shift of distribution range centroids (Fig. 2a, Extended Data Table 2). In contrast, pond cypress (*Taxodium ascendens*) had the lowest velocity of all ($1.5 \text{ km} \cdot \text{decade}^{-1}$), followed by water-elm (*Planera aquatica*; $4.5 \text{ km} \cdot \text{decade}^{-1}$) and sweetgum (*Liquidambar styraciflua*; $4.5 \text{ km} \cdot \text{decade}^{-1}$). Our velocities of tree species range shifts are generally consistent with those reported in the previous studies (Extended Data Table 3). Few boreal tree species have ever been assessed in terms of shifting velocity, and here, we found that boreal tree species' ranges are shifting much faster than

temperate ones. In terms of direction, 36 out of 150 species shifted northwards, 34 eastwards, 27 southwards, and 53 westwards in the past 50 years (Extended Data Table 2).

At the forest-type level, we found that the range of Sitka spruce—western hemlock forest (W-A) shifted with the highest velocity at $327.8 \text{ km} \cdot \text{decade}^{-1}$ (Fig. 2b). Among the top six fast-shifting forest types, three were in the boreal forest biome (B-A, B-B, and B-D, see Extended Data Table 1 for forest type names), two were in the eastern mixed forest biome (E-A and E-K), and one was in the Pacific-coastal forest biome (W-B) (Extended Data Table 4). The remaining forest types shifted at a speed lower than $100 \text{ km} \cdot \text{decade}^{-1}$. In terms of the direction of shift, nine out of 43 forest types shifted westwards, 16 eastwards, 11 southwards, and seven northwards in the past 50 years (Extended Data Table 4).

Overall, forest-type range shifts differed substantially from tree species range shifts (*i.e.*, the average range shift of constituent tree species) in terms of velocity (Figs. 3, 4). On average, forest-type ranges shifted at $86.5 \text{ km} \cdot \text{decade}^{-1}$, more than three times as fast as the weighted average of their constituent tree species ($28.8 \text{ km} \cdot \text{decade}^{-1}$) across the continent at the grid level (Figs. 3b, 4c). For more than 75% of forest types, the range shifts at the forest-type level substantially outpaced the average range shifts of constituent tree species, and only 10 out of 43 forest types moved more slowly than their constituent tree species in terms of range shifts (Fig. 4c, Extended Data Table 4). In the boreal and Great Lakes regions, the velocity of forest-type range shifts exceeded that of tree species range shifts by $200 \text{ km} \cdot \text{decade}^{-1}$ or more (Fig. 3b). Along the Rocky and Appalachian Mountains, forest type ranges shifted with a lower velocity than the ranges of their constituent tree species (Fig. 3b).

The portfolio hypothesis of range shifts

The marked difference in the range shift velocity between forest type and constituent tree species is mainly attributable to *the portfolio effect*. We derived the following hypothesis from Markowitz's portfolio theory of investment¹⁰ to quantify the difference in range shifts between forest types and constituent tree species. Tree species range shift was represented by the geographic centroid shift of its suitable habitat range. Both boundary and centroid shifts can be relevant indicators of range shifts for both forest types and their constituent species. Forest type boundary shifts simply depict the minimum of each constituent species' boundary shift. As such, they will often reflect the slowest species' range boundary shift. Instead, the range centroid of a forest type reflects the distribution of its most representative and abundant/dominant species, capturing the primary function and service of this forest type.

Let $a_i(\mathbf{x})$ be the relative abundance of species i at spatial location x (demarcated by coordinates of latitude and longitude). The cumulative relative abundance of species i over space x is $\sum_x a_i(x) = A_i$, and the geographic centroid of species i 's range can be calculated as the weighted mean of x , $c_i = \sum_x x \cdot a_i(x) / A_i$. The relative abundance of a forest type at location x is the sum of its constituent species' relative abundance at the location, $a(x) = \sum_{i \in G} a_i(x)$, where G represents the set of all species of this forest type. The cumulative relative abundance of this forest type can be computed as $\sum_x a(x) = A$; let $p_i = A_i / A$, and the geographic centroid of the forest type can be calculated as $c = \sum_x x \cdot a(x) / A = \sum_{i \in G} c_i \cdot p_i$. By the Leibniz product rule of calculus, we have

$$\Delta c = \sum_{i \in G} \Delta c_i \cdot p_i + \sum_{i \in G} c_i \cdot \Delta p_i. \quad (\text{eq.1})$$

Because $\sum_{i \in G} p_i = 1$ and thus $\sum_{i \in G} \Delta p_i = 0$, the latter term of eq. 1 equals the covariance between species' centroids and the change in their cumulative relative abundance: $\text{cov}(c_i, \Delta p_i) = E(c_i \cdot \Delta p_i) - E(c_i) \cdot E(\Delta p_i) = \sum_{i \in G} c_i \cdot \Delta p_i$.

Notably, the shift in a forest type's centroid (Δc) is driven not only by the weighted mean of centroid shifts at the species level ($\sum_{i \in G} \Delta c_i \cdot p_i$), but also, counterintuitively, by the covariance ($\text{cov}(c_i, \Delta p_i)$) that inflates or deflates the centroid shift of the forest type (Extended Data Fig. 1). This covariance term, which we call *the portfolio effect*, can attribute to a difference between forest-type range shift and the range shift of its constituent tree species. We therefore made the following hypothesis: when the range shift of a forest type and its constituent tree species are measured along a given direction, a positive covariance ($\text{cov}(c_i, \Delta p_i)$) will inflate the magnitude and velocity of the forest-type range shift along this direction, while a negative covariance will reduce the magnitude and velocity along this direction (Extended Data Fig. 1). Our finding that the forest-type range shifts differed substantially from species range shifts provides a strong support for the portfolio hypothesis.

In most cases, portfolio effects are expected to be positive because species at the front of a forest-type range (*i.e.*, in the direction of forest-type range shift) often have increasing abundances due to preferential allocation to dispersal and reproduction, while species at the rear of forest-type range are decreasing in abundance, reflecting the compounded effect of constituent species' mortality and recruitment on the centroid shift^{14,15}. Positive portfolio effects provide a mechanistic underpinning of our finding that, across the North American continent, forest-type range shifts generally outpaced tree species range shifts (Figs. 3b, 4c). In some cases, negative covariance terms pervade, leading to reduced forest-type range shift, such as in some forests across the Rocky and Appalachian Mountains (Fig. 3b). In these montane forest types, constituent species increase their relative abundances in the rear edge, where investments in competitive traits are likely to dominate, even if the species centroids drift towards the front edge (Extended Data Fig. 1).

Various factors in complex interactions are attributable to species abundance dynamics, leading to positive or negative portfolio effects. While climate change (e.g., increasing temperature and precipitation changes) is commonly considered the major driver of species abundance dynamics and associated range shifts^{1,2,6}, climate change-induced disturbances (e.g., fires and disease outbreaks) and human disturbances (e.g., logging and land use changes) can further accelerate the dynamics of species abundance¹⁶⁻¹⁹. Although it is out of scope of this study to assess the determinants behind species abundance dynamics, we utilized non-climate predictor variables, including human footprint²⁰ (Extended Data Table 5), to account for the impacts of potential disturbances.

Impacts of forest-type range shifts

There are profound impacts of forest-type range shifts on forest biodiversity and associated ecosystem functioning, food, water, energy security²¹⁻²⁴, human well-being²⁵, and socioeconomic value²⁶. Forest-type range shifts can jeopardize the sustainability of local forest industries, making them more vulnerable to timber price fluctuations²⁷. It can also inflate timber procurement ranges and increase transportation costs, causing significant downstream financial implications with serious welfare and economic consequences comparable to the impact of COVID-19 on transportation and logistics²⁸. Furthermore, the collective human experiences of rural communities embedded within these forested landscapes have strong ties to surrounding forest types. From the Sitka spruce—western hemlock forests in the Pacific Northwest to the oak—pine forests along the Appalachians (Extended Data Table 1), the change of native forests is threatening the customs, identities, and culture of indigenous²⁹ and other local communities, and is jeopardizing the non-timber forest products supply and overall environmental justice³⁰. Rapid shift of forest type places an urgent call upon human communities, especially rural populations, to adapt their cultural norms and relationships with surrounding forests.

Our finding that a majority of forest types shifted faster than their constituent tree species due to positive portfolio effects suggests that the impacts of tree species' range shifts under global change on forest ecosystem functioning and services may be grossly underestimated. Forest ecosystem functioning^{31,32}, productivity³³, phenology, and population turnover^{34,35} are directly related to tree species composition and other forest characteristics^{31-33,36}. Therefore, existing adaptive forest management regimes, which are based primarily on individual species range projections and associated environmental and social aspects^{37,38}, have likely underestimated the impacts of global change (including climate change, land use change, invasive species regimes, habitat fragmentation, and forest degradation). For instance, in the central United States, a diminishing supply of various white oak species, such as white oak (*Quercus alba*) and bur oak (*Q. macrocarpa*), caused by the shift of oak-dominated forests (Extended Data Table 4) is threatening the entire bourbon industry³⁹, a staple of American culture and tradition. As forest-level change (25% reduction in Appalachian oak–pine forest range, Extended Data Table 1) was far more alarming than species-level change (e.g., 12.5% reduction in *Q. alba* range and 6% increase in *Q. macrocarpa* range, Extended Data Table 2), missing the forest for the trees for their range shift patterns can greatly reduce the capability and preparedness of local forest industry and communities to face global change through disruptions in timber supply chains and ecosystem benefits.

The divergent range shift patterns between forest types and tree species observed here represent only a snapshot of a more prominent trend seen in geological time scales. Forests, because of their sensitivity to changes of tree species compositions, have over the millennia exhibited shorter life spans than individual species⁴⁰. Positive portfolio effects provide an urgently needed scientific basis for a new paradigm of adaptive forest management and conservation in mitigating the impacts of rapid forest transformation under climate change.

References

1. Boisvert-Marsh, L., Périé, C. & de Blois, S. Shifting with climate? Evidence for recent changes in tree species distribution at high latitudes. *Ecosphere* **5**, 1-33 (2014).
<https://doi.org:10.1890/ES14-00111.1>
2. Sittaro, F., Paquette, A., Messier, C. & Nock, C. A. Tree range expansion in eastern North America fails to keep pace with climate warming at northern range limits. *Global Change Biology* **23**, 3292-3301 (2017). <https://doi.org:10.1111/gcb.13622>
3. Woodall, C. W. *et al.* Selecting tree species for testing climate change migration hypotheses using forest inventory data. *Forest Ecology and Management* **259**, 778-785 (2010). <https://doi.org:10.1016/j.foreco.2009.07.022>
4. Woodall, C. W. *et al.* An indicator of tree migration in forests of the eastern United States. *Forest Ecology and Management* **257**, 1434-1444 (2009).
<https://doi.org:10.1016/j.foreco.2008.12.013>
5. Zhu, K., Woodall, C. W. & Clark, J. S. Failure to migrate: lack of tree range expansion in response to climate change. *Global Change Biology* **18**, 1042-1052 (2012).
<https://doi.org:10.1111/j.1365-2486.2011.02571.x>
6. Fei, S. *et al.* Divergence of species responses to climate change. *Science Advances* **3**, e1603055 (2017). <https://doi.org:10.1126/sciadv.1603055>
7. Kelly, A. E. & Goulden, M. L. Rapid shifts in plant distribution with recent climate change. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 11823-11826 (2008). <https://doi.org:10.1073/pnas.0802891105>
8. Lenoir, J., Gegout, J. C., Marquet, P. A., de Ruffray, P. & Brisse, H. A significant upward shift in plant species optimum elevation during the 20th century. *Science* **320**, 1768-1771 (2008). <https://doi.org:10.1126/science.1156831>

9. Sharma, S. *et al.* North American tree migration paced by climate in the West, lagging in the East. *Proceedings of the National Academy of Sciences of the United States of America* **119** (2022). <https://doi.org/10.1073/pnas.2116691118>
10. Markowitz, H. M. Portfolio selection. *Journal of Finance* **7**, 77-91 (1952).
11. Chesson, P., Donahue, M. J., Melbourne, B. A. & Sears, A. L. in *Metacommunities: spatial dynamics and ecological communities* (eds M. Holyoak, M. A. Leibold, & R. D. Holt) Ch. 6, 279-306 (2005).
12. Hui, C., Fox, G. A. & Gurevitch, J. Scale-dependent portfolio effects explain growth inflation and volatility reduction in landscape demography. *Proceedings of the National Academy of Sciences of the United States of America* **114**, 12507-12511 (2017). <https://doi.org/10.1073/pnas.1704213114>
13. Schindler, D. E., Armstrong, J. B. & Reed, T. E. The portfolio concept in ecology and evolution. *Frontiers in Ecology and the Environment* **13**, 257-263 (2015). <https://doi.org/10.1890/140275>
14. Burton, O. J., Phillips, B. L. & Travis, J. M. Trade-offs and the evolution of life-histories during range expansion. *Ecology Letters* **13**, 1210-1220 (2010). <https://doi.org/10.1111/j.1461-0248.2010.01505.x>
15. Rumpf, S. B. *et al.* Range dynamics of mountain plants decrease with elevation. *Proceedings of the National Academy of Sciences of the United States of America* **115**, 1848-1853 (2018). <https://doi.org/10.1073/pnas.1713936115>
16. Brice, M. H., Cazelles, K., Legendre, P., & Fortin, M. J. Disturbances amplify tree community responses to climate change in the temperate–boreal ecotone. *Global Ecology and Biogeography* **28**, 1668-1681 (2019). <https://doi.org/10.1111/geb.12971>

17. Brice, M. H., Vissault, S., Vieira, W., Gravel, D., Legendre, P., & Fortin, M. J. Moderate disturbances accelerate forest transition dynamics under climate change in the temperate–boreal ecotone of eastern North America. *Global Change Biology* **26**, 4418–4435 (2020). <https://doi.org/10.1111/gcb.15143>
18. Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A. Z., & Schepaschenko, D. G. Boreal forest health and global change. *Science* **349**, 819–822 (2015). <https://doi.org/10.1126/science.aaa9092>
19. Seidl, R. *et al.* Globally consistent climate sensitivity of natural disturbances across boreal and temperate forest ecosystems. *Ecography* **43**, 967–978 (2020). <https://doi.org/10.1111/ecog.04995>
20. Venter, O. *et al.* Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications* **7**, 12558 (2016). <https://doi.org/10.1038/ncomms12558>
21. Gitay, H., Suarez, A. & Watson, R. Climate change and biodiversity. (International Panel on Climate Change, 2002).
22. Kremen, C. & Merenlender, A. M. Landscapes that work for biodiversity and people. *Science* **362**, eaau6020 (2018). <https://doi.org/10.1126/science.aau6020>
23. Neilson, R. P. *et al.* Forecasting Regional to Global Plant Migration in Response to Climate Change. *BioScience* **55**, 749–759 (2005). [https://doi.org/10.1641/0006-3568\(2005\)055\[0749:Frtgpm\]2.0.Co;2](https://doi.org/10.1641/0006-3568(2005)055[0749:Frtgpm]2.0.Co;2)
24. Wellstead, A. & Howlett, M. Assisted tree migration in North America: policy legacies, enhanced forest policy integration and climate change adaptation. *Scandinavian Journal of Forest Research* **32**, 535–543 (2017). <https://doi.org/10.1080/02827581.2016.1249022>

25. IPBES. Report of the plenary of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services on the work of its sixth session. (IPBES, 2018).
26. Hanewinkel, M., Cullmann, D. A., Schelhaas, M.-J., Nabuurs, G.-J. & Zimmermann, N. E. Climate change may cause severe loss in the economic value of European forest land. *Nature climate change* **3**, 203-207 (2013). <https://doi.org/10.1038/nclimate1687>
27. Zhou, M. Input substitution and relative input price variability in timber markets. *Canadian Journal of Forest Research* **51**, 339-347 (2021). <https://doi.org/10.1139/cjfr-2020-0338>
28. Polzin, S. & Choi, T. COVID-19's effects on the future of transportation. (2021).
29. Chamberlain, J. L. *Assessment of nontimber forest products in the United States under changing conditions*. Vol. 232 (Forest Service, 2018).
30. Fleetwood, J. Social justice, food loss, and the Sustainable Development Goals in the era of COVID-19. *Sustainability* **12**, 5027 (2020). <https://doi.org/10.3390/su12125027>
31. Cardinale, B. J. *et al.* The functional role of producer diversity in ecosystems. *American Journal of Botany* **98**, 572-592 (2011). <https://doi.org/10.3732/ajb.1000364>
32. Loreau, M. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* **91**, 3-17 (2000). <https://doi.org/10.1034/j.1600-0706.2000.910101.x>
33. Liang, J. *et al.* Positive biodiversity-productivity relationship predominant in global forests. *Science* **354** (2016). <https://doi.org/10.1126/science.aaf8957>
34. Pecl, G. T. *et al.* Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. *Science* **355** (2017). <https://doi.org/10.1126/science.aai9214>
35. Zhu, K., Woodall, C. W., Ghosh, S., Gelfand, A. E. & Clark, J. S. Dual impacts of climate change: forest migration and turnover through life history. *Global Change Biology* **20**, 251-264 (2014). <https://doi.org/10.1111/gcb.12382>

36. Paquette, A. & Messier, C. The effect of biodiversity on tree productivity: from temperate to boreal forests. *Global Ecology and Biogeography* **20**, 170-180 (2011).
<https://doi.org/10.1111/j.1466-8238.2010.00592.x>
37. Iverson, L. R., Prasad, A. M., Peters, M. P. & Matthews, S. N. Facilitating adaptive forest management under climate change: A spatially specific synthesis of 125 species for habitat changes and assisted migration over the eastern United States. *Forests* **10**, 989 (2019). <https://doi.org/10.3390/f10110989>
38. Millar, C. I., Stephenson, N. L. & Stephens, S. L. Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* **17**, 2145-2151 (2007). <https://doi.org/10.1890/06-1715.1>
39. Conrad, A. O. *et al.* Threats to Oaks in the Eastern United States: Perceptions and Expectations of Experts. *Journal of Forestry* **118**, 14-27 (2019).
<https://doi.org/10.1093/jofore/fvz056>
40. Williams, J. W., Shuman, B. N., Webb III, T., Bartlein, P. J. & Leduc, P. L. Late-quaternary vegetation dynamics in North America: Scaling from taxa to biomes. *Ecological Monographs* **74**, 309-334 (2004). <https://doi.org/10.1890/02-4045>

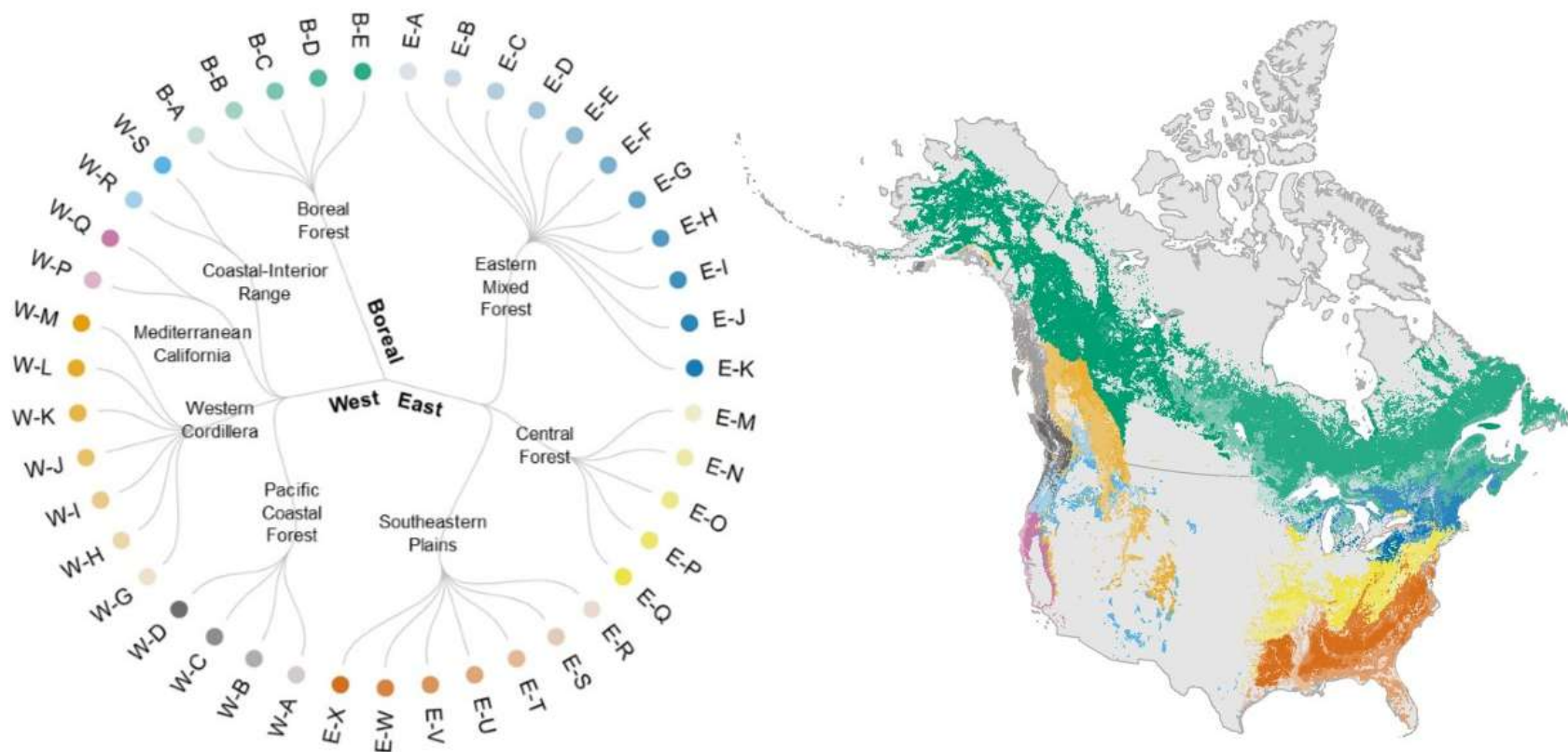


Figure 1. We classified forested areas across North America into 43 forest types in eight forest biomes and three arch-biomes (East, West, and Boreal) following the existing algorithms. See Extended Data Table 1 for the definition of forest types and constituent tree species. Colors in the circular dendrogram corresponds to those in the map of forest type distribution range.

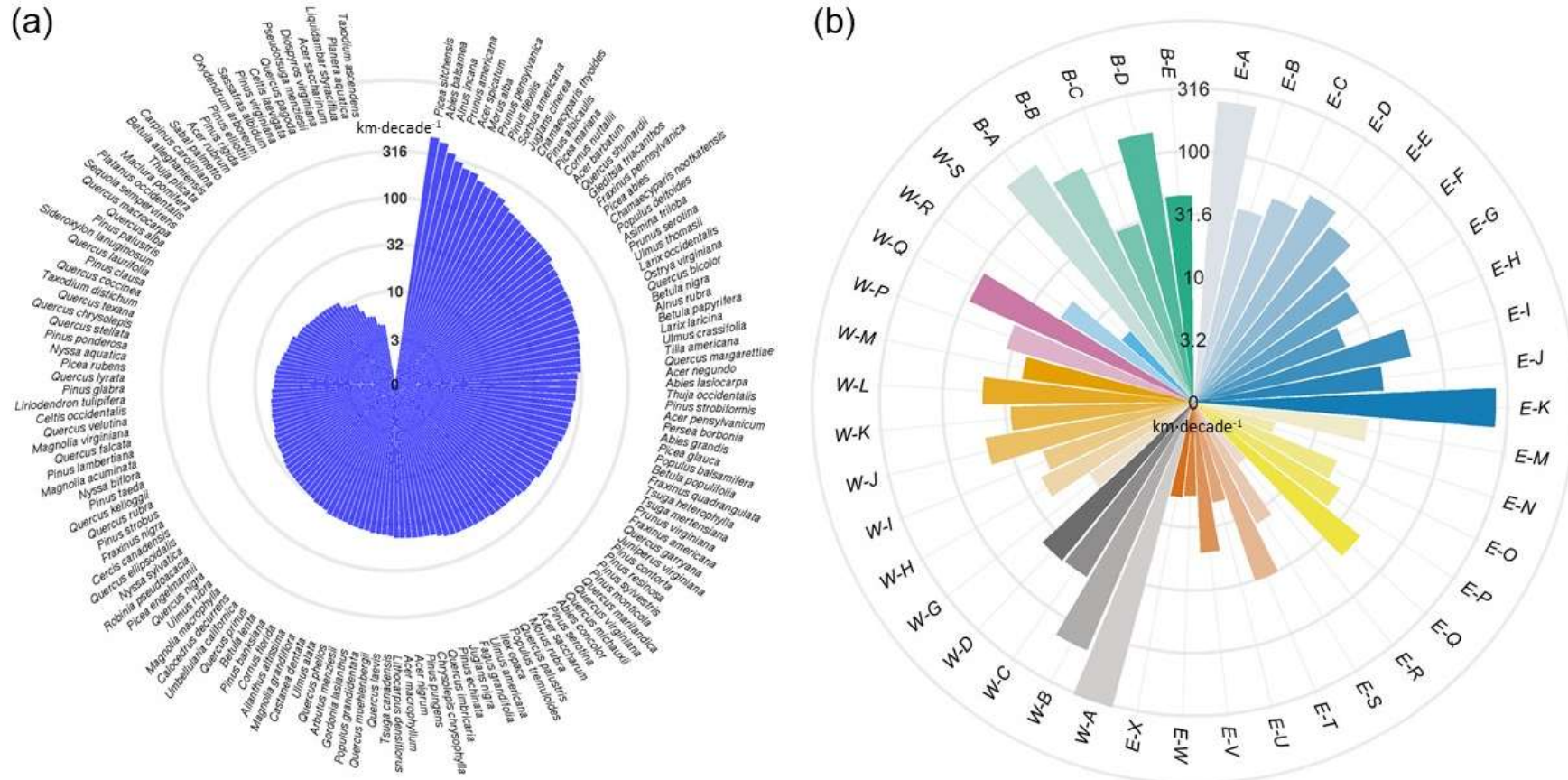


Figure 2. The velocity of (a) tree species range shifts and (b) forest-type range shifts. Velocity of shifts (here in logarithmic scale) is defined as the distance between past and present centroids of range in kilometers per decade ($\text{km} \cdot \text{decade}^{-1}$). See Extended Data Table 1 for the definition of forest types and constituent tree species.

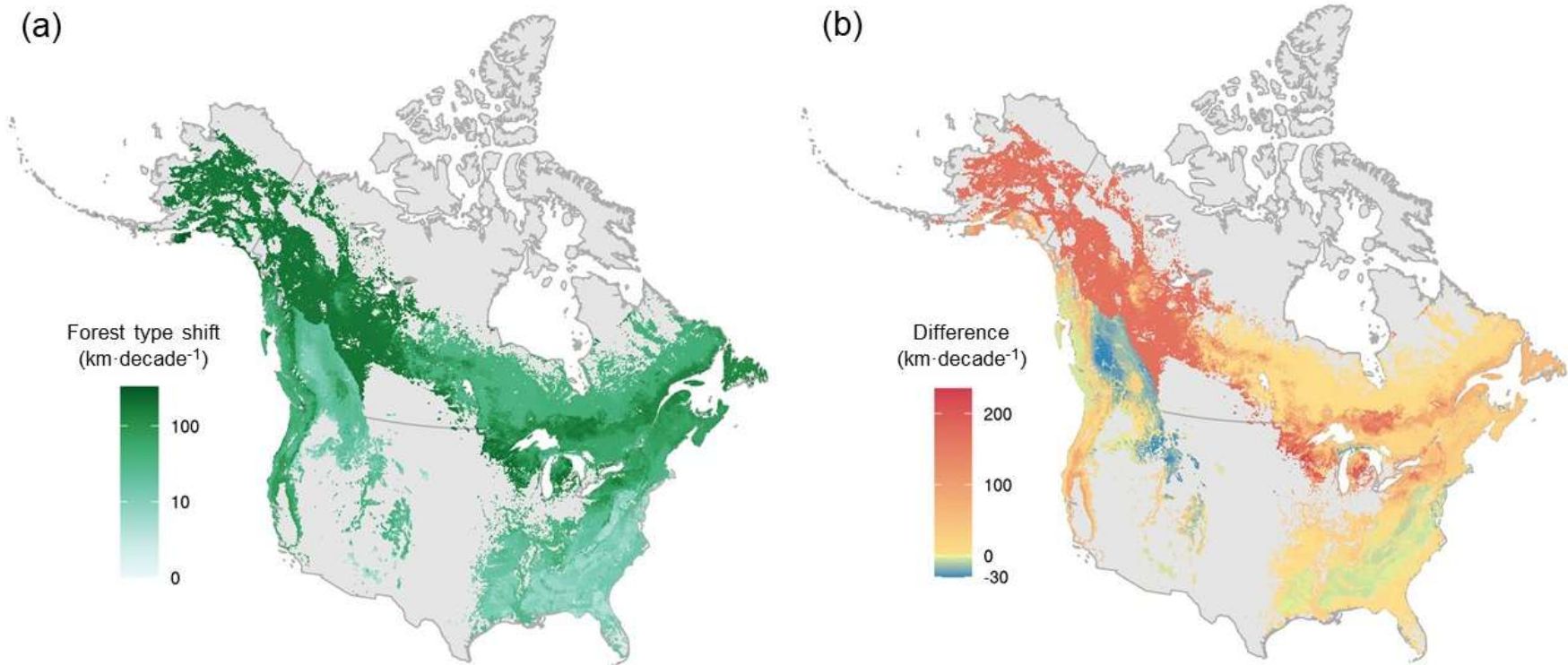


Figure 3. The velocity of forest-type range shift and the difference in velocity between forest types and the weighted mean of their constituent species across the continent, mapped at a 0.025° resolution. (a) The velocity of forest type at the grid level. (b) The difference in shift velocity between forest types and the weighted mean of their constituent species at the grid level, with warm colors representing areas where forest-type range shifts outpaced species range shifts, and cold colors representing areas where species range shifts outpaced forest-type range shifts.

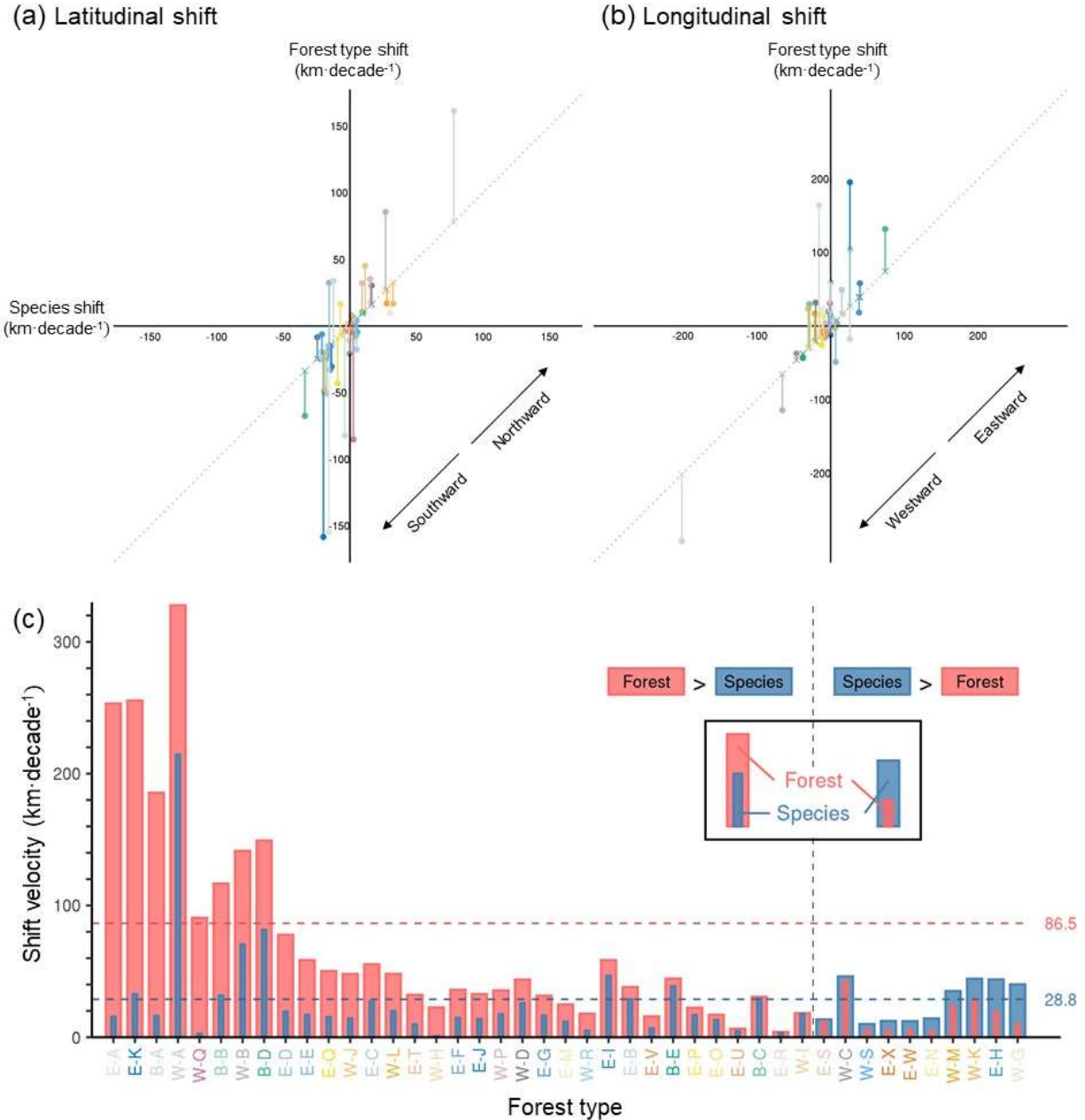


Figure 4. The difference between forest-type range shifts and tree species range shifts. Scatter plots show the velocity of forest type vs. tree species range shift velocity, in terms of latitudinal (a) and longitudinal (b) shift of geographic centroids, with positive values representing northward (a) and eastward (b) shifts and negative values southward (a) and westward (b) shifts. Vertical line segments represent the difference between the velocity of forest-type range shifts and tree species range shifts, along latitude (a) and longitude (b). The length of these segments is identical to the portfolio effect. (c) A comparison between the velocity of forest type and tree species range shift velocity, regardless of the direction. The horizontal dotted lines represent the mean velocity of forest type and tree species shifts in pink and blue, respectively. The mean velocity represents a grid-level velocity (*i.e.*, Fig. 3a for forest type). To ease identification of various forest types, axis text colors of the Panel (c) are consistent with Figs. 1 and 2b.

Methods

Definition and classification of forest type

Since certain tree species are often found together in natural forest communities, various assemblages of tree species imply different types of forest communities which support differed types of plants, wildlife⁴¹, and microbiomes⁴². A forest type represents a distinctive assemblage of tree species distributed across a wide geographical range⁴¹, which in some studies is also referred to as a forest region^{43,44}, a tree species assemblage⁴⁵, or a forest community⁴⁶. The classification of forest types provides important references for forest management, conservation, climate-change mitigation, and restoration⁴¹. Following an established forest type classification algorithm^{43,45}, we classified forested areas across the North American continent into 43 forest types in eight forest biomes and three arch-biomes (Fig. 1, Extended Data Table 1, see Supplementary Information for details).

While existing forest type classifications is limited to either Canada or the United States⁴³⁻⁴⁶, our study supports ongoing and future international collaborations in forest management and climate actions⁴⁷, with a consistent continental-wide data-driven forest type classification scheme. Nevertheless, our classified forest types are generally compatible with existing forest type classifications for the North American Continent⁴³⁻⁴⁶.

Data integration

For this study, we compiled and integrated *in situ* forest-tree data from independent and standard forest inventories. Data for the United States came from the Forest Inventory and Analysis (FIA)⁴⁸ and the Cooperative Alaska Forest Inventory (CAFI)⁴⁹. Data for Canada came from two independent sources: permanent sample plot networks^{36,50} and Canada's National

Forest Inventory ground plot network^{51,52}. See Supplementary Information for a detailed description of each data.

We derived the following data integration protocol to harmonize the different forest inventory datasets described above into consistent continental data frames. From each dataset, we obtained tree-level information for all the trees with a minimum diameter at breast height (DBH) of 1 cm. We grouped these tree-level records by the year of inventory and compiled one data frame for 2000–2019 and another data frame for 1970–1999. For each period, we summarized tree-level information into a plot-level species abundance matrix. We calculated, for each sample plot, the importance value index (IVI hereafter) for a species, which is the sum of the percent number of stems and the percent basal area for the species. Frequently used in forestry research as a typical measure of species abundance^{43,45,53}, IVI equally weighs the number of stems and basal area of a particular species, and ranges from 0 to 200.

The final continental data frames consisted of plot identification and coordinates, as well as the IVIs of all tree species present on each plot. The plots were widely distributed across the forested areas of the continent (Extended Data Fig. 2). For the 1970-1999 data frame, because some trees in the genera of *Aesculus*, *Amelanchier*, *Carya*, *Crataegus*, *Halesia*, *Malus*, and *Salix* were recorded only to the genus level, we also calculated the IVIs of these genera (Extended Data Table 2). To harmonize the past and present survey data, we derived the average species IVI of all plots located within a 0.025 by 0.025-degree (approximately 3 by 3 km) grid cell in each past and present plot-level dataset, which is a reasonable aggregation regardless of the distribution of species IVI (see Supplementary Information). Each forested grid cell had a minimum 10% canopy cover based on the global forest range map⁵⁴, in accordance with FAO's definition of 'forest'⁵⁵.

Our study region encompassed 1,004,358 grid cells of forested area across North America, with a total of ~5 million km². The tropical regions of North America, *i.e.*, Mexico, Central America, and the Caribbean, were not included in this analysis due to a lack of remeasured *in situ* data. Our study region covered 92 terrestrial ecoregions⁵⁶ across the United States and Canada. These ecoregions were grouped into three distinct arch-biomes: West (39 ecoregions), East (33 ecoregions), and Boreal (20 ecoregions, Extended Data Fig. 2). For each arch-biome and time frame (2000–2019 and 1970–1999), we classified forest type (see Supplementary Information) and quantified distribution ranges of forest types and constituent tree species separately.

Range shifts of tree species

Following the formulation of the portfolio hypothesis, the first step to quantify forest-type range shifts is to determine constituent species' range shift patterns, which consisted of two steps: creating a spatially continuous map of species *i*'s relative abundance ($a_i(x)$) at location *x* (*i.e.*, grid latitude and longitude) across the continent and quantifying its geographic centroid shift (Δc_i). To estimate a species' relative abundance, we first mapped species IVI across the 4.9 million-km² study region using random forests model and 38 predictor variables. For each arch-biome (West, East, and Boreal) and time frame (2000–2019 and 1970–1999), only species with sufficient sample size (≥ 60 grids) in both time periods were included (Extended Data Table 2). Random forests are a non-parametric ensemble learning approach⁵⁷, which combines a variant of decision trees and an additional level of randomness by bootstrapping sub-data and different sets of predictor variables to mitigate the multicollinearity issues that most statistical models face⁵⁸. We used the “randomForest” package in R (version 4.0.4)^{59,60}. Following previous research⁵³, we reported the mean predicted IVI of all decision trees for each species or zero for species with zero median and a coefficient of variation no less than 2.75 among all predicted values of

decision trees. For each species, we built 20 random forests models to calculate an average IVI in each grid cell.

The predictor variables we compiled consisted of 17 climate variables⁶¹⁻⁶⁴, 13 topographic variables⁶⁵, seven soil variables⁶⁶, and human footprint²⁰. These predictor variables were derived from open access satellite-based remote sensing and ground-based survey data layers, all of which have a nominal resolution of 1 km. Detailed information on the predictor variables is available in Extended Data Table 5. We used the “Hmisc” package in R to impute missing data in those predictor variables⁶⁷.

Based on the estimated species IVI, we calculated species relative abundance ($a_i(x)$) by calculating percent IVI for each species in each grid cell. We then calculated the cumulative relative abundance ($A_i = \sum_x a_i(x)$) and geographic centroid ($c_i = \sum_x x \cdot a_i(x)/A_i$) for each species. The direction and velocity of species range shift were calculated based on the displacement between the past and present geographic centroids using the “sp” and “sfsmisc” packages in R^{68,69}. In this study, the direction was measured in azimuth, the angle between past and present geographic centroids around the same horizon (*i.e.*, altitude was not considered), ranging from 0 to 360° measured from the North direction. We also determined the total area of each species’ range as the sum of the grid area weighted by the species’ relative abundance. Grid area was estimated using the “raster” package in R⁷⁰.

Range shifts of forest types

We predicted the distribution ranges of forest types by first considering two candidate imputation models: random forests and support-vector machines. Support-vector machines are supervised learning models which construct a hyperplane or set of hyperplanes in a high- or infinite-dimensional space to help analyze data for classification and regression analysis⁷¹. We

used the “e1071” package in R with the default hyperparameter setting⁷². For random forests, we used the default hyperparameter setting of the “randomForest” package in R⁵⁹ and the same set of predictor variables as described in *Range shifts of tree species*.

To assess the performance of the imputation model in mapping forest types across the continent, we conducted a rigorous 80/20 cross-validation using bootstrapping. In each iteration, we used stratified sampling to split the entire dataset into the training (80%) and testing (20%) sets and conducted the combination of under-sampling and oversampling of the training set for both random forests and support-vector machines to balance the sample size for all classes. Stratified sampling was conducted using the “caret” package in R⁷³, and under-sampling and oversampling were conducted using the “UBL” package⁷⁴. Based on five random iterations with sample replacement in each of the 20 repetitions, we calculated the 95% confidence interval of classification accuracy, the Kappa statistic, and elements of the confusion matrix. For each candidate imputation model, the output was a matrix of class probability from five iterations. We chose the forest type of majority vote from the five iterations, and thus, our final output was a matrix of class probability from the 20 repetitions. Based on how many repetitions, out of 20, returned the given forest type, we calculated percent forest type in each grid cell. The random forests model was 10–17% and 11–20% more accurate in terms of overall accuracy and the Kappa statistic, respectively, compared with the support vector machine model (Extended Data Fig. 3). Therefore, we selected random forests as the final imputation model. The confusion matrices based on random forests models were based on the number of cases in class prediction, standardized in percentage (Extended Data Figs. 4, 5). For the present dataset, the coastal redwood—tanoak forest (W-P) had the highest classification accuracy (88%, Extended Data Fig. 4), and the red maple—hardwood forest (E-F) had the lowest one (18%, Extended Data Fig. 4) among all forest types.

Following the formulation of the portfolio hypothesis, we calculated forest type-level shift (Δc), weighted sum of species-level shifts ($\sum_{i \in G} \Delta c_i \cdot p_i$), and the covariance (the portfolio effect, $\text{cov}(c_i, \Delta p_i)$) for each forest type along the latitudinal and longitudinal gradient. See Supplementary Information for determining the correspondence of past (1970–1999) and present (2000–2019) forest types. Along each respective gradient, the weighted sum of species range shifts ($\sum_{i \in G} \Delta c_i \cdot p_i$) and covariance term ($\text{cov}(c_i, \Delta p_i)$) precisely matches a forest-type range shift (Δc). In a two-dimensional space with latitude and longitude combined, we also derived the velocity of a forest-type range shift in kilometers per decade and azimuth angle by calculating the distance between past and present forest type centroids using “sp” and “sfsmisc” packages in R^{68,69}. This forest-type range shift can be visualized as a vector in a two-dimensional space of latitude and longitude, as a resultant of two composing vectors: species-level vector and covariance vector. Quantifying the length of these two vectors (*i.e.*, velocity) is not practical due to the earth’s curvature, yet we aimed to approximate it by calculating the distance between past forest type centroid and the point to where the vector heads, both in degrees and kilometers. Finally, to expand the velocity of forest-type and species range shifts to a grid level, we weighted the velocity of each forest type by the percent forest type presence in each grid cell. Average percentage of past and present forest type was used.

Data and code availability

The forest inventory data used in this study includes publicly available data: Forest Inventory and Analysis (FIA) (<https://apps.fs.usda.gov/fia/datamart/datamart.html>), permanent sample plots for Québec (<https://www.donneesquebec.ca/recherche/dataset/placettes-echantillons-permanentes-1970-a-aujourd-hui>), and Canada’s National Forest Inventory (<https://nfi.nfis.org/en>). Grid-level input data with tree species IVI for each region (West, East,

and Boreal) for each time frame (2000–2019 and 1970–1999) to reproduce the results, as well as the output forest type and biome maps (geoTIFF layers), are available through figshare (<https://doi.org/10.6084/m9.figshare.22825313.v1>). The predictor variables used in this study are all openly available; climate covariates are available through WorldClim (<https://www.worldclim.org/data/worldclim21.html>), CHELSA (<https://chelsa-climate.org/bioclim/>), and Trabucco & Zomer (2019) (https://figshare.com/articles/dataset/Global_Aridity_Index_and_Potential_Evapotranspiration_ET0_Climate_Database_v2/7504448/4), topographic covariates are available through EarthEnv (<https://www.earthenv.org/topography>), soil covariates are available through WISE30sec (<https://data.isric.org/geonetwork/srv/eng/catalog.search#/metadata/dc7b283a-8f19-45e1-aaed-e9bd515119bc>), and human footprint layer is available from Venter et al. (2016) (<https://doi.org/10.5061/dryad.052q5>). More details about the predictor variables are in Extended Data Table 5.

Methods References

41. Perry, C. H., Finco, M. V. & Wilson, B. T. Forest Atlas of the United States. 54 (U.S. Department of Agriculture, Forest Service,, Washington, D.C., 2022).
42. Steidinger, B. S. *et al.* Climatic controls of decomposition drive the global biogeography of forest-tree symbioses. *Nature* **569**, 404–408 (2019). <https://doi.org/10.1038/s41586-019-1128-0>
43. Dyer, J. M. Revisiting the deciduous forests of eastern North America. *BioScience* **56**, 341–352 (2006). [https://doi.org/10.1641/0006-3568\(2006\)56\[341:RTDFOE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[341:RTDFOE]2.0.CO;2)
44. Rowe, J. S. (ed Canadian Forestry Service Department of the Environment) (1972).

45. Costanza, J. K., Coulston, J. W. & Wear, D. N. An empirical, hierarchical typology of tree species assemblages for assessing forest dynamics under global change scenarios. *PLoS One* **12**, e0184062 (2017). <https://doi.org:10.1371/journal.pone.0184062>
46. Knott, J. A., Jenkins, M. A., Oswalt, C. M., & Fei, S. Community-level responses to climate change in forests of the eastern United States. *Global Ecology and Biogeography* **29**, 1299-1314 (2020). <https://doi.org/10.1111/geb.13102>
47. FAO & UNEP. The State of the World's Forests 2020. Forests, biodiversity and people. (FAO and UNEP, Rome, Italy, 2020).
48. Burrill, E. A. *et al.* The Forest Inventory and Analysis Database: database description and user guide version 9.0.1 for Phase 2. 1026 (U.S. Department of Agriculture, Forest Service, 2021).
49. Malone, T., Liang, J. & Packee, E. C. Cooperative Alaska forest inventory. (US Department of Agriculture, Forest Service, Pacific Northwest Research Station, 2009).
50. Chen, H. Y., Luo, Y., Reich, P. B., Searle, E. B. & Biswas, S. R. Climate change-associated trends in net biomass change are age dependent in western boreal forests of Canada. *Ecology Letters* **19**, 1150-1158 (2016). <https://doi.org:10.1111/ele.12653>
51. National Forest Inventory. Canada's National Forest Inventory – ground plot data. (Canada's National Forest Inventory, 2011).
52. Zhang, Y., Chen, H. Y. H. & Taylor, A. R. Positive species diversity and above-ground biomass relationships are ubiquitous across forest strata despite interference from overstorey trees. *Functional Ecology* **31**, 419-426 (2017). <https://doi.org:10.1111/1365-2435.12699>

53. Iverson, L. R., Peters, M. P., Prasad, A. M. & Matthews, S. N. Analysis of climate change impacts on tree species of the eastern US: Results of DISTRIB-II modeling. *Forests* **10**, 302 (2019). <https://doi.org/10.3390/f10040302>
54. Hansen, M. C. *et al.* High-resolution global maps of 21st-century forest cover change. *Science* **342**, 850-853 (2013). <https://doi.org/10.1126/science.1244693>
55. FAO. Global forest resources assessment 2020. (Rome, Italy, 2020).
56. Olson, D. M. *et al.* Terrestrial ecoregions of the world: A new map of life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* **51**, 933-938 (2001). [https://doi.org/10.1641/0006-3568\(2001\)051\[0933:Teotwa\]2.0.Co;2](https://doi.org/10.1641/0006-3568(2001)051[0933:Teotwa]2.0.Co;2)
57. Breiman, L. Random forests. *Machine learning* **45**, 5-32 (2001). <https://doi.org/10.1023/A:1010933404324>
58. James, G., Witten, D., Hastie, T. & Tibshirani, R. *An introduction to statistical learning*. Vol. 112 (Springer, 2013).
59. Liaw, A. & Wiener, M. Classification and regression by randomForest. *R news* **2**, 18-22 (2002).
60. R: A language and environment for statistical computing (R Foundation for Statistical Computing, Vienna, Austria, 2021).
61. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International journal of climatology* **37**, 4302-4315 (2017). <https://doi.org/10.1002/joc.5086>
62. Karger, D. N. *et al.* in *Climatologies at high resolution for the earth's land surface areas* (Dryad Digital Repository, 2022).

63. Karger, D. N. *et al.* Climatologies at high resolution for the earth's land surface areas. *Scientific data* **4**, 1-20 (2017). <https://doi.org:10.1038/sdata.2017.122>
64. Trabucco, A. & Zomer, R. in *Global Aridity Index and Potential Evapotranspiration (ET0) Climate Database v2* (figshare, 2019).
65. Amatulli, G. *et al.* A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data* **5**, 180040 (2018).
<https://doi.org:10.1038/sdata.2018.40>
66. Batjes, N. H. Harmonized soil property values for broad-scale modelling (WISE30sec) with estimates of global soil carbon stocks. *Geoderma* **269**, 61-68 (2016).
<https://doi.org:10.1016/j.geoderma.2016.01.034>
67. Harrell Jr., F. Hmisc: Harrell miscellaneous. R package version 5.1-0. (2023).
68. Maechler, M. *et al.* Package 'sfsmisc'. (2023).
69. Pebesma, E. & Bivand, R. S. Classes and methods for spatial data: the sp package. *R news* **5**, 9-13 (2005).
70. Hijmans, R. & Van Etten, J. Raster: geographic data analysis and modeling. R package. (2020).
71. Vanpik, V. & Cortes, C. Support-vector networks. *Machine Learning* **20**, 273-297 (1995). <https://doi.org:10.1007/BF00994018>
72. Meyer, D. *et al.* e1071: misc functions of the department of statistics, probability theory group (formerly: E1071), TU Wien. *R package version 1* (2019).
73. Kuhn, M. *et al.* caret: Classification and regression training. R package version 6.0-86. (2020).
74. Branco, P., Ribeiro, R. P. & Torgo, L. UBL: an R package for utility-based learning. (2016).

Acknowledgements: We thank the Global Forest Biodiversity Initiative (GFBI) and Science-
i.org for facilitating the international research collaboration. We thank Mo Zhou and John B.
Dunning, Jr. for their feedback on this study.

Author contributions: Conceptualization, J.L., A.O.A., C.H., and N.P.; Methodology, A.O.A.,
J.L., and R.S.; Investigation, A.O.A., J.L., C.W.W., J.G.P.G., and T.O.; Writing – Original Draft,
A.O.A. and J.L.; Writing – Review & Editing, All; Supervision, J.L.

Declaration of interest: The authors declare no competing interests.

Funding: This work was supported by the U.S. Department of Agriculture’s (USDA)
Agricultural Marketing Service [grant numbers AM200100XXXXG007]; USDA National
Institute of Food and Agriculture McIntire Stennis project 1017711; Start-up Fund provided by
the Department of Forestry and Natural Resource and the College of Agriculture, Purdue
University; Department of Forestry and Natural Resources, Purdue University; Takenaka
Scholarship Foundation; Natural Sciences and Engineering Research Council of Canada [grant
numbers RGPIN-2019–05109, STPGP506284]; and Serra-Hunter Fellowship provided by the
Government of Catalonia.

Additional information: Correspondence and requests for materials should be addressed to
Jingjing Liang; 715 W. State St., West Lafayette, IN 47907, USA; albeca.liang@gmail.com;
001-765-496-0254. Supplementary Information is available for this paper