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Biodiversity recovery is slow following clear-cut harvest of boreal forests

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Boreal forests are important reservoirs of biodiversity, carbon and timber stocks. However, timber harvest can alter biodiversity in these forests without clear evidence on the duration needed for biotic groups to recover. Resilience of boreal forest biodiversity to clear-cut harvest was examined with a meta-analysis of 190 datasets from boreal and hemi-boreal forests of Europe/Russia and North America for arthropods, birds, small mammals, lichens, bryophytes and vascular plants. We modelled similarity of community composition between harvested and unharvested stands versus years post harvest. In approximately half of cases, predicted times for recovery to pre-harvest composition were ≤30 years. In other cases, recovery took much longer or had not occurred within the timeframe of our data; for example, in conifer forest: >100 years (bryophytes), >55 years (small mammals), ~95 years (lichens) and ~85 years (vascular plants). Saproxylic beetles showed no resilience within the 16 (conifer forest) or 29 (mixed forest) years post harvest for which we had data. Recovery generally took longer in conifer and mixed than in broadleaf forests, which always showed either resistance (bryophytes, vascular plants) or resilience with recovery within 12–25 years. Conserving biodiversity in boreal forests will require extended rotations, management for 'old forest' structural elements and areas protected from harvesting.

Disturbances are important drivers of forest structure, function, composition and biodiversity[1]. The concept of resilience provides a framework for predicting and understanding ecological dynamics following a disturbance[2] and can involve both the ability to maintain the pre-disturbance condition ('resistance') and/or the ability to return to that state ('resilience')[2–4]. Ecosystem dynamics following disturbance reflect: the nature of the disturbance, prevailing environmental conditions, species interactions and 'ecological memory' (that is, pre-disturbance ecological legacies; for example, surviving individuals or reproductive propagules, dead trees, nutrient pools, species adaptations)[2,4,5]. Together these factors drive post-disturbance dynamics, including whether and how the system can return to its pre-disturbance state[4,5]. Natural disturbances occur due to fires, windstorms, insect outbreaks and pathogens, but in managed forests, timber harvest is often the main disturbance[6]. Limited evidence suggests that a return to the 'pre-disturbance' condition (that is, 'recovery') after harvest could take decades or centuries, or forests could shift to a new (quasi-equilibrium) state[5–9]. To date, however, there has been a lack of meta-analyses testing

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ecological resilience theory by examining the post-harvest temporal dynamics of community composition for a variety of biotic groups to determine whether, and when, harvested forests might eventually recover to their pre-disturbance condition. Achieving targets to counter biodiversity loss and ensure sustainable forestry (United Nations Biodiversity Conference 2022 (COP15)-Target 10[10]) necessitates understanding harvest impacts[8,11,12] and use of the best available knowledge to inform biodiversity management (COP15-Target 12[10]). Thus, quantification of post-harvest ecological recovery of biodiversity is fundamental to land-use and conservation planning and biodiversity management[12–14]. Here we present a transatlantic analysis examining resistance and resilience, or lack thereof, of biodiversity following clear-cut harvest of boreal forests by comparing similarity of community composition between harvested and unharvested reference stands as a function of time since harvest.

Boreal (including sub- and hemi-boreal) forests represent ~30% of global forest area[15], 45% of timber stocks[16] and ~30% of terrestrial carbon stocks[1,17]. They provide habitats for a wide range of biota[12], supply many contributions to humanity[16] and are experiencing high rates of climatic warming[18]. Boreal forests are variously dominated by conifers, broadleaf trees or a mixture of the two with composition and structure reflecting natural-disturbance regimes[19–21]. Earlier successional stands are typically dominated by broadleaf species or shade-intolerant disturbance-adapted conifers; mixed woods are found at mid-successional stages while later-successional stages and regions with infrequent stand-replacing disturbances are characterized by shade-tolerant conifers[19–21]. Harvesting in the boreal often affects areas as large as those experiencing natural disturbances while also tending to concentrate on the most productive and biodiverse areas[6,12,22]. This, plus the dominance of even-aged silviculture systems (clear-cutting mature stands, soil scarification, planting, vegetation management, thinning) in boreal forest management, has led to concerns about their ecological sustainability[6,12,21,23,24]. Whereas boreal forest trees can achieve a size suitable for harvest by ~60–80 years of age, key ecological features such as large live trees rich in microhabitats and large standing snags and decayed downed wood take centuries to develop[23,25]. Many studies have provided evidence for negative effects of clear-cutting on boreal forest biodiversity, for example, refs. 12,26–28, with recent reviews suggesting that clear-cutting results in changes in community composition and species richness for several biota and that these effects can be long lasting (>50 years) (refs. 21,24). The vast majority of studies, however, are relatively short lived, typically focus on a single biotic group and often examine metrics such as species richness or abundance, which can increase or decrease following harvest, complicating interpretations of responses[14,21]. Thus, we still lack a comprehensive understanding of the long-term effects of clear-cutting on biodiversity, especially for patterns of temporal dynamics of community composition[14,21].

We tested for resistance and resilience of boreal forest biodiversity following clear-cut harvest by characterizing post-harvest temporal trends in similarity of community composition between harvested stands and unharvested reference forests. Our analyses included a wide variety of biotic groups and used datasets from three boreal forest stand types (conifer dominated, mixed conifer broadleaf, broadleaf dominated) from across the transatlantic. Most studies examined clear-cut harvest ('final felling'); a few had very low levels of retention. Comparable mature forest (older than the regional typical harvest rotation age) was the reference; these were almost never 'old-growth' forest (much older than typical rotation age or defined as 'old growth' by the authors). We focused on recovery of community composition because it reflects both species presence and relative abundance, thus capturing species turnover[9,14]. Our results reflect recovery of community composition and did not provide insight into species that are rare/uncommon or of particular conservation concern. 'Full recovery' was defined as when the community similarity of harvested versus unharvested reference stands was, on average, comparable to similarity among reference stands.

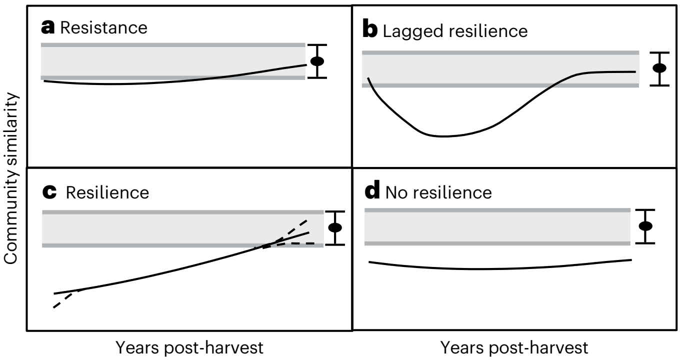


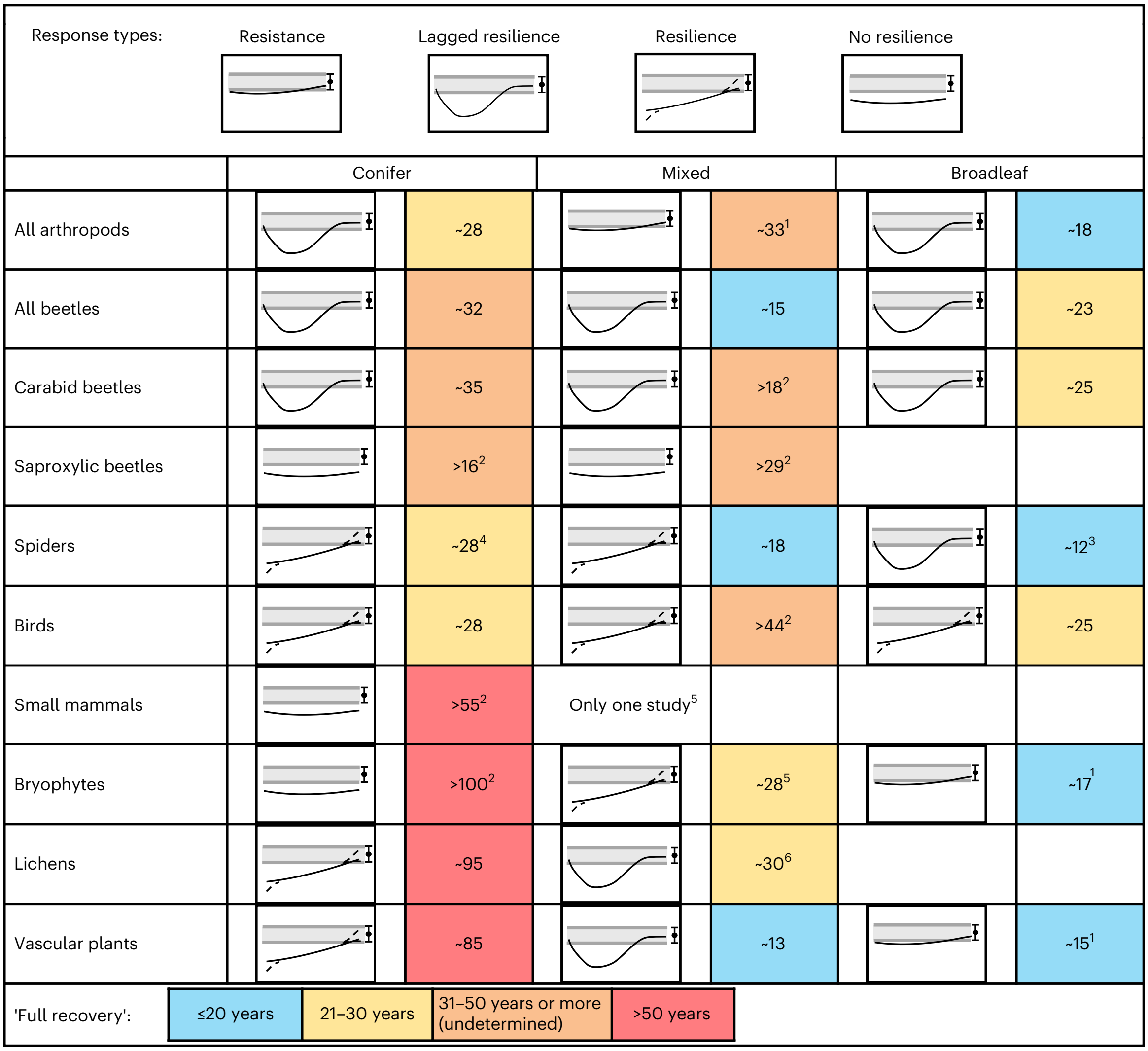
Fig. 1 | Generalized temporal patterns observed for post-harvest recovery of boreal forest biodiversity. On the *y* axis is community similarity (Chao–Jaccard Index) between harvested and unharvested mature forest stands. The *x* axis represents the number of years post harvest. The line represents the general curve shape from the generalized additive mixed model (GAMM). The point with error bars at the right and the grey rectangle represents the mean similarity (and 95% confidence interval) among reference replicates. 'Full recovery' was defined as the year post harvest when the GAMM smoother intersects with the lower confidence interval of the reference (Fig. 4). **a**, Resistance: no significant temporal trend and the GAMM curve overlaps the lower confidence interval of the reference sometime during the post-harvest period. **b**, Lagged resilience: a decrease in harvested vs reference similarity in the earlier years post harvest followed by an increase, potentially to the point defined as 'full recovery'. **c**, Resilience: low harvested vs reference similarity in the initial post-harvest years followed by a linear (or curvilinear as indicated by the dotted lines) increase, potentially to 'full recovery'. **d**, No resilience: no significant temporal trend and the GAMM curve falls consistently below the lower confidence interval of the mean reference versus reference similarity.

We hypothesized: (1) post-harvest recovery would be nonlinear with a temporal lag post harvest due to effects of ecosystem memory as individual species responses to disturbance accumulate[5,29]; (2) biota associated with ecological features of mature, natural-disturbance-origin forests (for example, large live or dead trees or downed decayed deadwood) would show poorer post-harvest recovery because these features are reduced post harvest[23,27,30]; (3) biotic communities of conifer forests (which are often later-successional) would show poorer recovery than the earlier successional mixed or broadleaf forests since post-harvest microenvironmental changes are probably more dramatic in conifer forests, particularly for those that naturally experience gap dynamics or low-severity fire[19], and post-harvest canopy redevelopment takes longer than in the other forest types[20].

Results

Patterns of post-harvest recovery

We observed four general temporal patterns of post-harvest response across 26 cases (biotic groups × forest types) (Fig. 1): (1) 'resistance': no significant temporal trend and the curve from the generalized additive mixed model (GAMM) of harvested vs reference community similarity versus years post harvest (YPH) overlapped with the confidence interval for similarity among unharvested reference stands sometime post harvest; (2) 'lagged resilience': significant temporal trend with an initial decline in harvested versus reference similarity followed by an increase, potentially to the point meeting the definition of 'full recovery' (intersection of the GAMM curve with the lower 95% confidence interval of mean reference versus reference similarity); (3) 'resilience': significant trend from lower harvested vs reference similarity immediately following harvest followed by a more or less linear trend of increasing similarity, potentially to the point of 'full recovery'; (4) 'no resilience': no



	Conifer	Mixed	Broadleaf
All arthropods	~28	~33[1]	~18
All beetles	~32	~15	~23
Carabid beetles	~35	>18[2]	~25
Saproxylic beetles	>16[2]	>29[2]	
Spiders	~28[4]	~18	~12[3]
Birds	~28	>44[2]	~25
Small mammals	>55[2]	Only one study[5]	
Bryophytes	>100[2]	~28[5]	~17[1]
Lichens	~95	~30[6]	
Vascular plants	~85	~13	~15[1]

'Full recovery': ≤20 years | 21–30 years | 31–50 years or more (undetermined) | >50 years

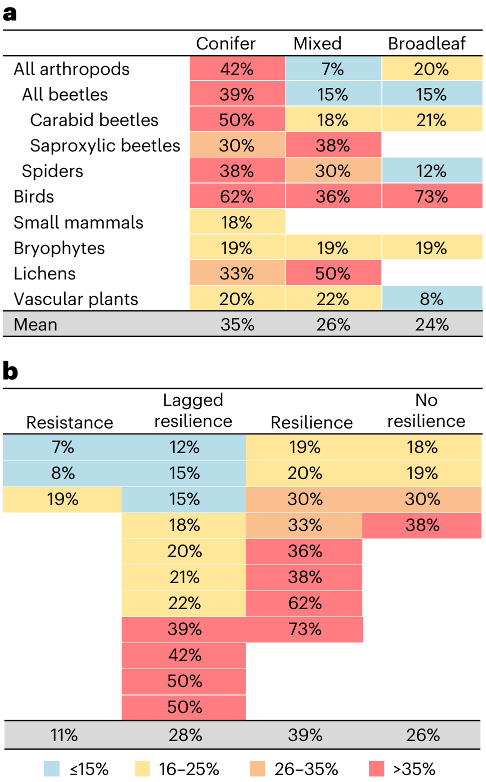
Fig. 2 | Modelled response type and years to 'full recovery' of community composition following clear-cutting. The embedded figure at the top shows the different recovery pattern types: the solid black line represents the general form of the smoother from the GAMM of harvested vs reference similarity (*y* axis) as a function of years post harvest (YPH; *x* axis); the point with error bars at the right and the grey rectangle represents the mean similarity (and 95% confidence interval) among reference replicates (Fig. 1). The main body provides the recovery curve type and estimated mean YPH for 'full recovery' for each biotic group and forest type. Supplementary Fig. 1 provides full results and Supplementary Table 6 provides details of analyses including number of datasets per biotic group and forest type and significance of the GAMM. [1]Although the pattern met the definition of 'resistance', we still note the YPH that met the definition of 'full recovery'; [2]'full recovery' did not occur within the maximum period for which we had data. [3]Only two datasets, only to 28 YPH. [4]No datasets between 16 and 51 years, only one dataset for each of 51 and 52 YPH. [5]One study, three datasets, only to three YPH. [5]No datasets between 22 and 50 YPH and only one dataset for 50 YPH. [6]No datasets between 10 and 50 and only one dataset for 50 YPH.

significant temporal trend, the GAMM curve of harvested vs reference community similarity fell consistently below the lower 95% confidence interval of mean reference versus reference similarity.

Responses of communities, and evidence for resistance or resilience, varied among biotic groups and forest types; however, harvesting consistently resulted in a change in community composition. The modelled similarity between harvested and unharvested reference forests always fell lower than the average similarity among reference stands at sometime post harvest (almost always significant; Fig. 2, Supplementary Table 6 and Supplementary Fig. 1). At the lowest point on the GAMM curve, harvested versus reference similarity was, on average, 29% lower than the average similarity among reference stands (Fig. 3).

The vast majority of cases showed resilience (8/26) or lagged resilience (11/26) with very few instances of resistance (3/26 cases) or no resilience (4/26 cases) (Fig. 2). Modelled time to 'full recovery' often occurred within ~35 years post harvest (18/26 cases) but sometimes took ≥ 50–100 years (Fig. 2). In 6/26 cases 'full recovery' had not been reached within the time period for which we had data (Fig. 2). There was considerable variation in the underlying data, with many instances of very low similarity between harvest and reference replicates, even many decades post harvest (Fig. 4). The maximum decline in mean harvested versus reference similarity (100 − lowest point on GAMM curve as a percentage of mean similarity among reference stands) was greater for cases showing resilience (average ~39%) than for other response patterns (lagged resilience: 28%, no resilience: 26%, resistance: 11%) (Fig. 3).

As hypothesized, recovery was poorer for conifer and mixed forests than for broadleaf forests. The modelled time to 'full recovery' in conifer forests was ~28 to >100 years with 3/10 cases showing no resilience. Recovery in mixed forests took ~13 to >44 years with 1/9 cases for each of no resilience and resistance. Broadleaf forests reached 'full recovery' within ~12 to ~25 years with no instances of no resilience and two cases of resistance (Fig. 2). The maximum average decline in community similarity between harvested and reference stands was higher in conifer (35%) than in mixed (26%) or broadleaf (24%) forests (Fig. 3).



a

	Conifer	Mixed	Broadleaf
All arthropods	42%	7%	20%
All beetles	39%	15%	15%
Carabid beetles	50%	18%	21%
Saproxylic beetles	30%	38%	
Spiders	38%	30%	12%
Birds	62%	36%	73%
Small mammals	18%		
Bryophytes	19%	19%	19%
Lichens	33%	50%	
Vascular plants	20%	22%	8%
Mean	35%	26%	24%

b

Resistance	Lagged resilience	Resilience	No resilience
7%	12%	19%	18%
8%	15%	20%	19%
19%	15%	30%	30%
	18%	33%	38%
	20%	36%	
	21%	38%	
	22%	62%	
	39%	73%	
	42%		
	50%		
	50%		
11%	28%	39%	26%

🟦 ≤15% 🟨 16–25% 🟧 26–35% 🟥 >35%

Fig. 3 | Modelled maximum decline in community similarity of clear-cut boreal forests compared to the unharvested reference. a,b, Maximum post-harvest decline in similarity between harvested and unharvested reference forest: 100 − (similarity at the lowest point on the GAMM smoother of harvest vs reference similarity as a percent of the mean reference vs reference similarity) for each biotic group in each forest type (**a**) and list of values by recovery curve type (**b**) (Fig. 2 and Supplementary Fig. 1). Means appear on the bottom row in (**a**) and (**b**).

Results by biotic group

'All arthropods', 'all beetles', carabid beetles and spiders almost always (11/12 cases) showed resilience or lagged resilience. They also tended to have shorter times to predicted 'full recovery' (12 to 35, and in one case >18 years) and—for mixed and broadleaf forests—slightly less divergence from the reference (7% to 30% decline, average 17%) than other biotic groups. For these biotic groups the modelled time to 'full recovery' tended to be longer in conifer than broadleaf forests (~28 to ~35 versus ~12 to ~25 years; Fig. 2). In mixed forests, 'all arthropods' showed resistance, 'all beetles' and carabid beetles showed lagged resilience and spiders showed resilience with times to predicted 'full recovery' of ~15 to 18 years, or in one case of >18 years (not including the one case of resistance) (Fig. 2 and Supplementary Fig. 1a,b,c,e). In contrast, saproxylic beetles showed no resilience in both conifer and mixed forests with no evidence of a trend towards recovery within the 16 (conifer forest) and 29 (mixed forest) years post harvest that we had data for (Fig. 2 and Supplementary Fig. 1d). The maximum average decline in harvested vs reference similarity was slightly greater for carabid beetles (average of 30% across forest types), saproxylic beetles (34%) and spiders (27%) than for 'all arthropods' or 'all beetles' (~23% for both) (Fig. 3).

Birds in all forest types showed resilience, with modelled times to 'full recovery' in conifer and broadleaf stands of ~28 and ~25 years post harvest, respectively, while predicted 'full recovery' in mixed forests had not yet been reached by 44 years, the maximum age for which we had data (Fig. 2 and Supplementary Fig. 1f). The maximum average decline in harvested vs reference similarity was higher for birds than in other biotic group (36–73%, average of 57%; Fig. 3). Small mammals in conifer-dominated forests showed no resilience with no evidence of a trend towards 'full recovery' within the 55 years for which we had data; however, the maximum decline in harvested vs reference similarity was only ~18% (Fig. 3, Fig. 2 and Supplementary Fig. 1g).

Bryophytes, lichens and vascular plants all tended to show poor recovery, with particularly long times to recovery in conifer forests (all ≥85 years) (Fig. 2). Bryophytes showed no resilience in conifer forest with no evidence of recovery within the 100 years post harvest for which we had data. In mixed forests they showed resilience with predicted 'full recovery' by ~28 years while in broadleaf forests, they showed resistance (Fig. 2 and Supplementary Fig. 1h). The maximum average decline in community similarity for bryophytes was only ~19% (Fig. 3). Lichens in conifer-dominated forests showed resilience with modelled 'full recovery' taking ~95 years; the maximum decline in similarity was ~33% (Fig. 3 and Fig. 2). Lichens in mixed forests showed lagged resilience with a maximum decline in similarity of ~50% (Fig. 3 and Fig. 2). Their modelled time to 'full recovery' was ~30 years (Supplementary Fig. 1i). Vascular plants in conifer and mixed forests showed resilience and lagged resilience, respectively, with 'full recovery' predicted to take ~85 years in conifer forest but only ~13 years in mixed forests. In broadleaf forests vascular plants showed resistance (Fig. 2 and Supplementary Fig. 1j). The maximum average decline in community similarity for vascular plants was 8–22% (Fig. 3).

In some cases predictions of time to 'full recovery' should be taken with caution due to a paucity of data. For spiders in conifer forests, there were no data between 16 and 50 YPH; for bryophytes in mixed forests, no data between 22 and 50 YPH, and for lichens, no data between 10 and 50 YPH. In all three cases data for the latest time period came from only one study.

Discussion

This transatlantic meta-analysis showed that clear-cut harvest in boreal forests consistently resulted in divergence of community composition away from that of unharvested reference forests. There was evidence of resilience for most biotic groups and forest types. Modelled times to 'full recovery' were ~12 to 20 years in a few cases but more often ~25–35 years, or longer than the time period for which we had data. Indeed, in several cases predicted 'full recovery' took >55 and up to ~85, ~95 or >100 years.

As hypothesized, post-harvest recovery of community composition varied among biotic groups and forest types and was usually nonlinear, often showing a temporal lag (initial gradual decline in harvested versus reference community similarity with a subsequent increase). Our results support previous evidence for the strong effects of clear-cut forest harvest on biodiversity[6,21,24,27,28]. Substantial changes in the complement of species and their relative abundances after clear-cutting, at least in the short- or mid-term, were illustrated by the dramatic post-harvest divergence from the reference community composition. Interestingly, several of our modelled times to 'full recovery' correspond with the ~30–40 years reported for a variety of ecosystem function and biotic variables in forests globally[7], although that estimate was based on the authors' judgement on whether a system had recovered. Similarly for lowland tropical forests redeveloping after agricultural use, a recent study suggested that community composition for several biotic groups attained 75% similarity to old-growth forests within 30 years (ref. 14).

Variation in recovery patterns

Natural disturbances create forest landscapes with a mosaic of stand ages and types, each of which is important for biodiversity[12,31]. Many studies have demonstrated substantive differences in post-disturbance structure, function, and biodiversity between harvested forests and those following natural disturbances such as fire[26,31]. We chose to compare harvested forests to the mature forest reference condition because we consider harvesting to be an additional disturbance footprint.

The recovery patterns and predicted times to 'full recovery' we present are generalized expected responses, with much unexplained variation around the GAMM curves. Studies exploring the influence

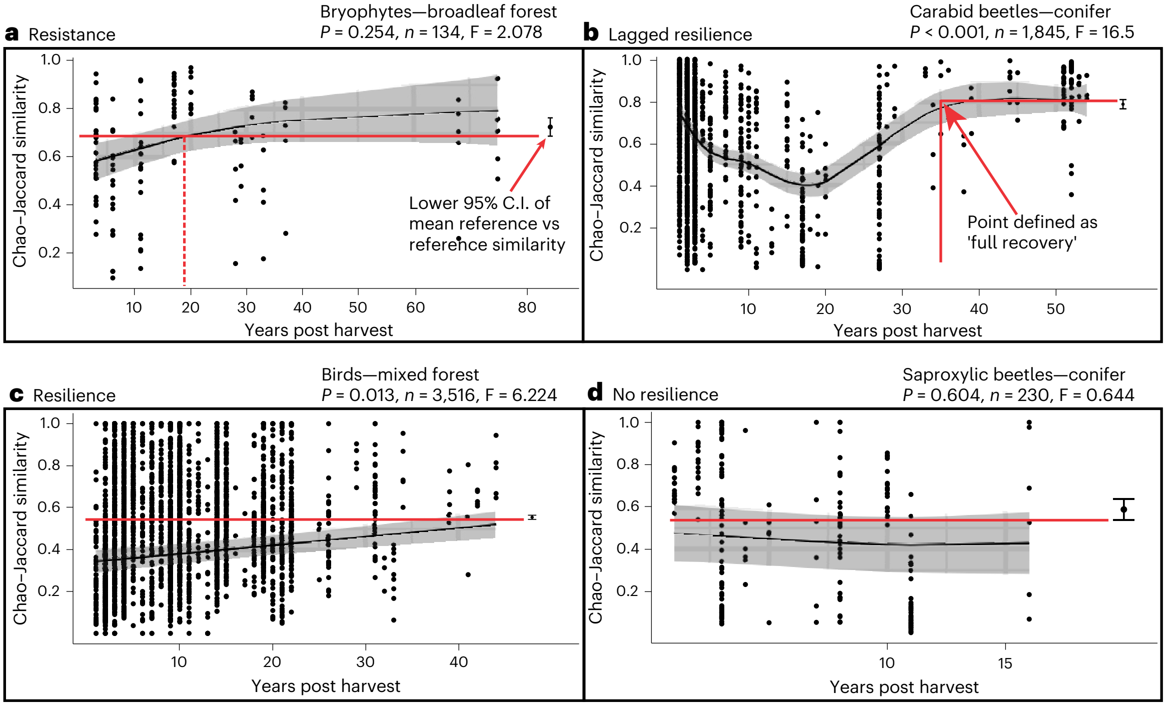


Fig. 4 | Example results for the different temporal recovery patterns observed post harvest for boreal forest biodiversity. On the *y* axis is community similarity (Chao–Jaccard Index) between harvested and unharvested mature forest reference stands. The *x* axis represents the number of years post harvest (YPH). The solid black line is the smoother from the generalized additive mixed model (GAMM) of harvested vs reference similarity as a function of YPH with the standard error around the smoother shown as the grey ribbon. The point with error bars at the right is the mean similarity (and 95% confidence interval (C.I.)) among unharvested mature forest stands with the red horizontal line marking the position of the lower confidence interval. The vertical red line marks the YPH that meets the definition of 'full recovery' (if applicable), defined as the YPH when the GAMM smoother intersects the lower 95% confidence interval of the reference. The black dots are individual similarity values between harvested and reference replicates. **a**–**d**, Biotic group, forest type, *n* (number of harvest vs reference similarity values) and the *p*-value and F for the smoother are given for each post-harvest recovery curve type: resistance (line marking years to 'full recovery' is dashed) (**a**); lagged resilience (**b**); resilience (**c**); no resilience (**d**) (Fig. 1 and Supplementary Fig. 1 provide full results).

of modifying factors and contextual differences on responses would be most welcome (for example, forest site types, natural-disturbance regimes, post-harvest forest development, condition of surrounding landscape). The GAMM curve was particularly sensitive to cases with few data for intermediate time periods (for example, beetles in mixed and broadleaf forests) and estimates of 'full recovery' are necessarily imprecise because we had relatively few data for >30 years post harvest (Supplementary Table 4). Studies with data for multiple years post harvest were most often chronosequences. More datasets with long-term repeated measurements for >30 years post harvest would help refine estimates of 'full recovery' and further improve our understanding of longer-term effects of clear-cut harvest[21].

In the vast majority of cases there was some evidence of resilience (resilience or lagged resilience) with a pattern of increasing community similarity between harvest and reference over time post harvest. This is in concordance with evidence of recovery for productivity, nutrient cycling and tree and understory plant diversity following harvest[26] and may be particular to the boreal forest, which often experiences a natural-disturbance regime dominated by stand-initiating disturbances such as fire. There was considerable variation, however, in the timing of recovery and the underlying data included many individual examples that showed no evidence of recovery even 50–100 years post harvest (that is, harvest vs reference similarity values ~ 0; Supplementary Fig. 1b,h–j: all beetles, bryophytes, lichens and vascular plants in conifer forests). Very poor resilience for individual sites can probably be explained by composition and structure of the post-harvest forest, which strongly reflects harvesting practices and silvicultural treatments[12,18,32]. Recovery was probably facilitated by redevelopment of the understory, shrub and sapling layers, which are particularly rapid in broadleaf and mixed forests, providing nesting and foraging habitat for birds[33,34]. This probably also explains why the greatest divergence in similarity of harvested and reference forests was greater for conifer than for broadleaf or mixed forests.

While we included only studies of clear-cutting (or very low retention), harvesting practices and silvicultural interventions have changed over time; thus, older post-harvest stands might have experienced management that was more, or less, intensive than more recent ones. This could be particularly influential for data representing longer periods post harvest and thus for estimated times to 'full recovery'. Future post-harvest biodiversity recovery will be strongly subject to climate change effects resulting in the potential for shifts in recovery trajectories[4,5,13]. Although planting can speed canopy redevelopment, particularly towards conifer dominance, re-establishing mixed woods and structurally complex forests by traditional silvicultural practices has proven challenging[35]. However, such forests are key reservoirs of biodiversity in boreal landscapes[36].

In several cases arthropods, and in some cases lichens and vascular plants, showed a lagged resilience response, such as would be expected due to ecosystem memory[5,29] or a lag in local extinction[37]. For ground beetles and forest floor spiders, such lags could be explained by some mature forest species persisting whereas open-habitat species colonize; with canopy closure at ~15–20 years, open-habitat species disappear while shade species remain at low levels[38,39] before eventually increasing to pre-harvest levels by 40–50 years (ref. 38). Lagged resilience for vascular plants in mixed forests could be explained by inclusion of perennial species associated with either a conifer or broadleaf canopy, allowing some species to persist through the changed environment following harvest[34,37].

Spiders, birds and in some cases lichens and vascular plants, showed resilience with no lag (that is, substantive post-harvest divergence from the reference forest composition immediately post harvest, followed by a gradual increase). In the case of spiders, this could be explained by *Pardosa* wolf spiders, which can increase by tenfold within 1–2 years post harvest[40]. For many bird species, this can be explained by them simply leaving an area when the habitat becomes unsuitable. For vascular plants in conifer and broadleaf forests, this is no doubt due to the direct disturbance of clear-cutting and associated changes in nutrient cycling, light and microclimatic conditions[41]. Such effects lead to rapid post-harvest increases in shade-intolerant, disturbance-adapted, early successional species accompanied by a rapid decline in shade-tolerant, later-successional species that naturally dominate the understory in conifer stands[37,41,42].

Whereas in just over half of cases (biotic groups × forest types) predicted times to 'full recovery' of community composition were within 30 years post harvest, important ecological differences remain between harvested and natural forests (for example, characteristics of deadwood, very large trees, population continuity) that could result in longer-term effects on biota[21,25,28]. Some features of mature forests (for example, large trees and snags, large decayed downed wood) take many decades to re-develop[25], delaying recovery of species such as cavity nesters[43], saproxylics and epiphytes[28,44]. As hypothesized, biota that showed no resilience or very long (>95 years) predicted times to 'full recovery' (saproxylic beetles, small mammals, bryophytes, lichens) were associated with ecological features that tend to be missing in post-harvest forests (large downed decayed dead wood, large live and dead trees)[25,45].

Bryophytes are sensitive to harvesting due to loss of key habitat features, desiccation and increased litterfall associated with broadleaf regeneration[46]. Their post-harvest recovery can be slow due to their scattered distribution, dispersal limitations and their substrate requirements[42,46]. For lichens, a long recovery time can be explained by a large set of specialist species inhabiting slowly developing habitat structures, combined with their slow and stochastic recolonization[21,44,47]. Small mammals had a relatively small decline in community similarity post harvest but no evidence of recovery within 55 years post harvest. This probably reflects species variation in response to harvesting, some being favoured by post-harvest conditions while others decline due to dependence on older-forest features (for example, structural complexity)[48]. For saproxylic beetles the lack of variation of deadwood during post-harvest succession may be crucial[28]. Whereas many saproxylic and epiphytic species can persist on logging residues and other residual coarse wood, these habitats tend to decline over time, leading to a lack of large-diameter logs of advanced decay stages, in turn hindering recovery[12,25]. Our results concur with studies showing that changes in community composition of saproxylic beetles, bryophytes and lichens following clear-cutting lasted more than 50 years (ref. 21).

Our results do not suggest that clear-cut harvest results in forests transitioning to an alternative state, as might be expected due to the loss of important pre-harvest habitat structures[49], if tree regeneration failed or composition shifted[50] or if a young post-harvest stand burned[51]. However, such transitions are certainly not precluded in particular cases, indeed we saw many individual examples for which similarity between harvested and reference stands was extremely low, even several decades post harvest (Fig. 4).

There were only three cases of resistance: 'all arthropods' in mixed forests, bryophytes and vascular plants in broadleaf forests. The first of these can probably be explained by pooling species with different niches, thus masking variation in responses. For example, a previous study found saproxylic beetles showed lagged resilience while non-saproxylic beetles seemed to demonstrate resistance[28]. The resistance of bryophytes and vascular plants in broadleaf forests probably reflects the dominance of these understory communities by early successional, disturbance-adapted species[34,37,42]. Forest floor mosses could survive post harvest due to their high ecological amplitude (for example, survival on remaining tree bases and decaying wood) while decreased seasonal litterfall post harvest enhances bryophyte survival and establishment[26,42]. Bryophyte species in broadleaf forests are also more adapted to drought and light than those in conifer stands[42]. Further, broadleaf tree species often regenerate very rapidly post harvest and this can help buffer ground vegetation from the effects of harvest-related soil disturbance and microclimate changes[34,42]. True epiphytic species will obviously decline sharply with logging as their habitat substrate is removed.

Our results reflect the sampling methods employed in the different studies (Supplementary Table 3). Rare species can easily be missed in standard inventory approaches[32,52], and some sampling methods for invertebrates or birds could include individuals using adjacent unharvested forest habitat[33]. Other than for birds, sampling did not address arboreal biodiversity (for example, epiphytic lichens, bryophytes, arthropods), which can be an important component of biodiversity that presumably increases along with canopy height and diversification[21,53,54]. Epiphytic lichens could need several hundred years to recover post harvest[45]. Our reference forest (no recent natural or anthropogenic disturbance) stands were primarily 80–150 years old; only three studies characterized the reference forest as 'old growth'. We excluded studies where the reference had been heavily managed, but for many European studies reference stands would have been lightly managed or selectively cut long ago[21]. Thus, we cannot comment on recovery of 'old growth' specialists, which comprise an estimated 10–20% of the forest species pool and depend on rarer ecological elements such as large live and dead trees, heterogeneous canopy and large, decayed downed wood[21,30,55]. Although frequent natural disturbances in boreal forests constrain the development and abundance of such features, a lack of them in managed forests is a major reason for the red-listing of species[21,23,28,47,55,56].

The poorer recovery of conifer and mixed, versus broadleaf, forests, and the greater decline in post-harvest similarity between harvested and reference conifer forests, has several possible explanations. Because evergreen conifers with dense foliage and persistent horizontally layered crowns tend to cast heavier shade than deciduous broadleaf trees their removal results in greater microenvironmental changes (that is, light, temperature)[57]. Furthermore, conifer forests in Europe naturally experience low-severity disturbances resulting in a multi-aged structure, whereas broadleaf forests are more often the product of stand-initiating disturbances[19,20]. Post-harvest silviculture often aims to return stands to their pre-harvest composition or another desired forest type[58]. Still, post-harvest canopy redevelopment might be slower in conifer and mixed forests because conifers often require planting and initially grow slowly, whereas broadleaf trees (aspen, birch) have pioneer characteristics such as prolific seed regeneration on disturbed sites, vegetative regeneration and rapid early growth[59], perhaps because they grow on more productive sites[3]. Also, broadleaf forests dominated by aspen or birch are more likely to return directly to a similar composition post harvest[20,60], whereas mixed or conifer stands might temporarily have higher broadleaf abundance[20,60–62].

Post-harvest recovery also reflects the availability and dispersal capacity of species in the regional pool, which, in turn, is affected by natural-disturbance regimes, harvesting footprint and associated fragmentation[63,64]. Disturbance-driven landscapes, such as the boreal, host biota that are early successional or generalists[65]; thus, they may have a good supply of colonizers. This could explain why many common boreal songbirds are resilient to moderate harvest levels[22]. Our results further support this. However, our results cannot provide insight into post-harvest responses for species that function at a larger landscape scale, nor landscape-scale cumulative effects of forest management (fragmentation, age structure, composition) or multiple cycles of harvesting and tending[11,12,21,23]. Negative impacts of these on biodiversity have been well documented[21,66], and forest biodiversity is likely to become increasingly impoverished in landscapes that have a longer history of forest management[25,56,64].

Implications for biodiversity conservation

Our results demonstrate clear impacts of harvesting on biodiversity in boreal forests. Although the biotic communities we studied often displayed resilience to clear-cutting, the estimated times to 'full recovery' for some biota were longer than the typical time before the next harvest, and there were many individual examples of a complete lack of recovery, even 50–75 years after harvest. Given existing forest rotation cycles, conservation of biodiversity in boreal forests could require extending rotation intervals or managing for 'old forest' structural elements retained after harvest (for example, large downed wood, large live and dead trees) and protection of some harvest-age forests from harvesting[6]. Our focus on similarity of community composition reveals average recovery but does not provide insight for rarer species. Future studies could employ a risk-based or precautionary approach that considers the possibility of reduced abundance or loss of species post harvest (particularly rare, threatened, species of conservation concern, common species) as decreased local diversity can also reduce ecosystem productivity and stability. Conservation of rare species, old-growth specialists and other biota sensitive to stand- or landscape-scale impacts of forest harvesting will require targeted approaches such as natural-disturbance-based management, partial cutting or retention forestry, mixed wood management, continuous cover forestry, multiscale forestry, conservation of biodiversity hotspots and preserving ecosystem memory[6,22,67,68].

Methods

Systematic review

We conducted a systematic review of the literature, searching the Web of Science, JSTOR, SCOPUS and Google Scholar databases for all available years to identify articles that reported on the influence of forest harvest on biodiversity outcomes in boreal forests. Specifically, we formulated a concatenated string of key search terms, as follows: (harvest* OR harvesting OR clearcut OR clearcutting OR clear-cut OR clear-cutting OR logging OR felling OR cutting) AND (*diversity, species AND (*diversity OR community OR composition OR assemblage OR species abundance OR cover)) AND (*boreal OR boreo-nemoral OR boreo-nemoral OR hemi-boreal). Records of all studies were saved to an Endnote database and the last date of access was 25 February 2020. This literature search yielded 1,922 articles after removal of duplicates. An update of the search on 22 July 2025 yielded 597 records after removal of duplicates.

For subsequent screening we utilized the following inclusion and eligibility criteria: (1) type of study: only studies based on field data records as opposed to a literature review, synthesis or modelling exercise; (2) location: only studies conducted in the boreal forest (including boreo-nemoral and hemi-boreal forests); (3) intervention: only studies including data on the effects of forest harvest, either clear-cut or partial harvest with very low retention (<10% of the original tree density, basal area or volume) and with no additional treatments such as prescribed burning, herbicide application or thinning (site preparation or planting were accepted); (4) comparator: study must include an appropriate non-intervention reference such as pre-harvest data or data from a comparable mature forest that had not previously been harvested (some studies with prior light interventions were included); (5) outcomes: the study must include data on the effects of harvest on forest biodiversity (including amphibians, birds, fungi, invertebrates, lichens, mammals, plants, reptiles, soil microorganisms) with data on community composition responses (data on abundances of individual species for a broad suite of species in a given biotic group); we excluded studies that did not report species-level abundances and those reporting only on tree composition or on stand structural elements (for example, coarse woody material), mortality, productivity or regeneration; (6) language: only studies written in the English language were considered; (7) data availability: because our key purpose was to identify studies that could provide data for subsequent quantitative analysis, the study must report or include relevant data (for example, raw or data summaries of species abundance) or suggest the possibility to obtain such information from authors. For this reason, review or synthesis papers were excluded unless they contained primary data. However, for all relevant review papers we searched their literature cited sections to find any additional papers.

Subsequent screening and critical evaluation were implemented in the Covidence platform (http://covidence.org). All 2,519 articles were screened on title and abstract by two individuals, independently, and scored for inclusion or exclusion based on the above criteria. When there was doubt or disagreement as to whether the article met the inclusion criteria, we erred on the side of inclusion at this stage. This was often the case when it was not possible, based on the title or the abstract, to tell whether appropriate data would be available, whether an appropriate reference stand was sampled or whether the level of harvesting was appropriate for inclusion. This screening of titles and abstracts identified 542 articles as potentially relevant.

The full text of these 542 articles was read to verify that they met the inclusion criteria described above and to assess quality. The quality assessment included whether the article: (1) clearly described the experimental design; (2) properly accounted for confounding effects (for example, site or forest type differing between treatments); (3) had true replication and (4) included the age post harvest. Each article underwent full-text screening by two reviewers independently. When there was uncertainty or disagreement, we erred on the side of inclusion. Through this process, we excluded 206 articles (Supplementary Table 1).

We added additional potential sources of data to the remaining 336 articles by checking the references cited sections of review or synthesis papers or later when contacted authors suggested other articles. Each article was carefully screened again before attempting to contact authors, to determine whether data could be acquired from the paper, supplementary materials or a data repository. Through this process, some additional studies were excluded for various reasons (Supplementary Table 2). For example, for theses, we attempted to find published papers that represented the same data and deferred to the published paper when possible. We also identified situations when two or more articles used the same data or similar data from the same study; in these cases we deferred to the more comprehensive dataset, seeking advice from authors when possible. We attempted to contact authors of all articles via email using the contact information in the published paper or by tracking them down through Google Scholar, ResearchGate, Web of Science, LinkedIn or a general search using Google. We tried to contact the corresponding author first, then deferred to other authors if necessary.

We requested data on: species abundances at the level of the true replicate (or sub-sample, in which case we averaged to the level of the replicate before analysis) for a broad suite of species within the defined biotic groups (arthropods, birds, small mammals, bryophytes, lichens, vascular plants) for harvested stands (clear-cut or low (<10%) level of retention) and comparable mature reference stands. In addition, we required data on location, forest region, forest type (conifer-, mixed, broadleaf- dominated), dominant tree species and years post harvest for harvested stands. Several biotic groups (amphibians, fungi, molluscs, reptiles, soil microorganisms) had too few data sources for meaningful analysis and were, therefore, excluded; this resulted in the exclusion of studies based on DNA data. For many articles, we were unable to contact the author(s) or they were unable to supply the data or sufficient meta-data for us to include them in analysis (Supplementary Table 2). For the studies identified in the updated search (July 2025), we concentrated on obtaining data that was readily available and that filled gaps in our existing datasets (time periods post harvest or biotic group).

Overall, we obtained data from 87 articles plus one unpublished study for a total of 190 datasets from boreal and hemi-boreal forests, primarily in North America and northern Europe, with two studies (11 datasets) from Russia (Supplementary Table 3 and Supplementary Fig. 2). Unfortunately, we were not able to obtain any data for studies from east of the Urals, including the Siberian taiga, and central and eastern Siberia and Mongolia. We also obtained very few studies in hemi-boreal and none from boreo-nemoral forests. The data we obtained were largely from studies focused on sites targeted for commercial forest harvesting; thus we have a paucity of data for more extreme (swamps, steep slopes, high elevation) sites. Our data generally included a similar number of datasets, with a similar range of years post harvest for each biotic group from Europe/Russia and North America (Supplementary Table 4). Exceptions were: a smaller range of years post harvest for spiders and small mammals from European studies; only one European dataset for spiders, birds and small mammals; and more North American datasets for understory vascular plants but fewer for lichens. While a wide range of years post harvest was represented in these data, relatively few datasets provided data for >30 years post harvest (Supplementary Table 4).

Data compilation and analyses

Although we were occasionally able to extract data from the original article, or a database associated with the article, in the vast majority of cases authors provided the data. In some cases, authors provided some unpublished data as well. We revised and formatted each dataset as required including: removing irrelevant treatments or data columns (for example, species richness or abundance for general categories of species), averaged sub-samples to the level of the replicate if necessary, transposed data format when necessary and re-organized or sub-divided data into separate datasets (for example, different forest types or biotic groups). Some studies provided multiple datasets (for example, data for different forest types or biotic groups, average of 2.2 datasets per study, range of 1–24; Supplementary Table 3). For subsequent quantitative analysis, each dataset was catalogued and the following meta-data extracted: study location; zone (boreal, hemi-boreal, boreal-nemoral); forest type (that is, conifer dominated, mixed conifer and broadleaf, broadleaf dominated); dominant tree species; range of years post harvest; age of the reference forest; biotic group(s) and subgroup(s); sampling method and number of datasets (Supplementary Table 3). The main datasets for analysis included data on abundance per species at the level of the replicate and years post harvest. Each study and dataset was given a unique code, as was each replicate (plot/stand) within each dataset. Data formatting was done either manually in Microsoft Excel (Microsoft Office Suite Version 16.0) or with the *dcast*() function from the reshape2 package[69] or the *t*() function in base R (version 4.2.2)[70].

Our approach to quantifying post-harvest recovery is adapted from Rozendaal et al.[9]. We calculated similarity in species composition between replicate stands/plots within a dataset using the Chao–Jaccard Similarity index. We chose this index because it compares abundances of shared and unshared species, reduces under-sampling bias by accounting for unseen, shared species and can account for large variations in species composition across reference forest plots within a site that results from local species turnover[71]. Further, biodiversity metrics, such as species richness, can increase or decrease following harvest[14,21] complicating interpretations of responses. Within each dataset, similarity values were calculated pairwise for harvested replicates (plots/stands) and their mature forest reference replicates (within a sampling year, if appropriate) and also pairwise among reference forest replicates (within a dataset). Chao–Jaccard dissimilarity values were calculated using the *dis.chao*() function from the CommEcol package[72] in R version 4.2.2[70] and then converted to similarity (1-dissimilarity).

The post-harvest biodiversity recovery curves were constructed through generalized additive mixed models (GAMMs) using the gamm4 function (vers 0.2-6[73]) in R version 4.2.2[70] to model the similarity between harvested and comparable reference plots/stands as a function of years post harvest. We constructed separate models for different biotic groups: 'all arthropods', 'all beetles', carabid beetles, saproxylic beetles, spiders, birds, small mammals, bryophytes, lichens and vascular plants. For each of these groups, we first ran a GAMM in which harvested versus reference similarity was the response variable, and years post harvest and forest type (conifer dominated, mixed, broadleaf-dominated) were predictor variables; replicate nested within dataset was included as a random variable. We tested for differences in the smoother among forest types using 'by = ' statements. On the basis of evidence that the temporal trend (GAMM smoother) varied among forest types (Supplementary Table 5), we conducted separate analyses by forest type, for each biotic group. We used a cubic spline and did not pre-define a maximum 'k' for the GAMMs; cross validation was used to determine the optimal amount of smoothing. For the analyses of each forest type separately, in most cases, the GAMM smoother was significant ($\alpha = 0.05$), indicating a significant post-harvest temporal trend in harvested vs reference similarity (Supplementary Table 6). The *predict* function was then used to produce the GAMM model outputs, including standard error around the smoother.

The mean similarity among mature forest reference replicates and the 95% confidence interval around that were calculated using the *summarySE* function in the Rmisc package in R[74]. To avoid greater influence by studies with a higher number of replicates, we first calculated the mean reference vs reference similarity for each dataset and then calculated the mean of those means. The ggplot2 package[75] was used to visualize the raw data (each replicate harvested vs reference similarity value), the GAMM model (smoother with standard error) and the mean similarity among reference replicates (with 95% confidence interval) for comparison. We defined the modelled time to 'full recovery' as the years post harvest at which the GAMM curve overlapped with the lower 95% confidence interval of the mean reference vs reference similarity. On the basis of a review of the different temporal patterns observed in the GAMMs, and their significance, we defined four general types of response (Fig. 1).

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Datasets used in the analysis (community similarity values with the studies anonymized because we did not receive permission from other authors to make their data publicly available) are available online in Mendeley[76].

Code availability

The R codes to calculate Chao–Jaccard Similarity and to run the GAMMs (all forest types combined and by forest type separately) are available via Github at https://github.com/EllenMacdonald-UofA/Post-harvest-forest-biodiversity-recovery.git.

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Author contributions

The first five authors are listed in order of contribution. S.E.M. and A.C.S.M. co-led the project including designing the study, contributing data, identifying and helping to acquire data from other studies, leading data analyses and interpretation and writing of the manuscript. S.S. played the major role in acquiring, organizing and analysing the data. S.B. devised the analytical approach and, together with S.-I.L. contributed data, assisted with acquisition of data from other studies, contributed to data analyses and interpretation and helped write the manuscript. The remaining 25 authors are listed alphabetically; all contributed data, provided input to data analysis and interpretation and to the writing the manuscript.

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Competing interests

The authors declare no competing interests.

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Community similarity values with datasets anonymized are available from Mendeley: Macdonald, S. E. & McIntosh, A.C.S.M. Boreal forest biodiversity recovery curves, Mendeley Data, (2026) https://doi.org/10.17632/yt42chsskj.1

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