



PERSPECTIVE

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Alpine forest genomics—advances in the research field and perspectives ahead

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Abstract

Key message Alpine or mountainous forest genomics research is rapidly moving from classic population genetic studies toward exploring population environmental adaptation to address climate vulnerabilities. For alpine conifers in particular, future progress in sustainable management relies heavily on overcoming the current bottleneck in the availability of genomic and experimental resources through targeted, interdisciplinary research efforts.

Context Mountainous forests are among the most vulnerable ecosystems to climate change. Over the past two decades, rapid advances in high-throughput sequencing have transformed research on mountainous tree species, enabling a transition from marker-based population genetic studies to genome-wide analyses of demography and adaptation.

Aims Here, we present a quantitative survey of how the field of mountainous or alpine forest genomics has evolved and provide future perspectives.

Methods We conducted a bibliometric analysis of 662 research articles published between 2000 and 2024, focusing on seven of the most important high-elevation European conifer species. Topic modeling and co-occurrence network analyses were used to identify major research topics and their dynamics in time. Moreover, members of the Alpine Forest Genomics Network (AForGeN, IUFRO Working Party 2.04.11) were asked in a survey to indicate future priorities and challenges of the field.

Results Our results show that publication activity has increased substantially after 2010 and that *Picea abies* (59%) was the most studied species. Topic modeling identified eight major research areas, and their temporal trends revealed a shift from genetic diversity and population structure studies towards environmental adaptation genomics. Co-occurrence analysis indicated two major clusters: population genetics and functional genomics research. Survey responses showed that there is an agreement that adaptation genomics will dominate the research of mountainous forests in the upcoming years, although the infrastructure, funding, and genomic resources remain major constraints to the development of this area of research.

Conclusions Our findings demonstrate a clear shift of the research field towards adaptation genomics, yet progress is hindered by a lack of genomic resources for non-model species and a gap in functional validation. To inform climate-resilient management of mountainous forests, the field must move beyond association patterns

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towards identifying the underlying mechanisms, e.g., by integrating ecophysiological and epigenetic studies. Such interdisciplinary efforts are essential to develop robust and actionable conservation and management strategies.

Keywords Mountains, Environmental adaptation, Conifer species, Population genetics, Genomic resources

1 Introduction

Middle- to high-altitude environments impose unique challenges to plants such as extreme temperatures, frequent (late) frosts, heavy snowfall, strong winds, high UV exposure, a short growing season and nutrient-poor soils, often in combination with rocky terrain. In particular, subalpine ecosystems located just below the treeline are dominated by coniferous forests in many parts of the world. In Europe, tree taxa such as *Larix*, *Picea*, *Abies*, and *Pinus* occur together with a mixture of shrubs and herbaceous plants. Species in these ecosystems have developed adaptations to cope with the harsh mountainous environment (Sun et al. 2025). These ecosystems are also characterized by a relatively high biodiversity with endemic animal and plant communities and play a crucial role in water and erosion regulation (Payne et al. 2017; Rahbek et al. 2019). Due to their sensitivity to environmental shifts that are above global averages (Mountain Research Initiative EDW Working Group 2015), they are early indicators of ecological shifts due to climate change. Insights into the ecological roles and evolutionary processes underpinning unique adaptive traits in high-elevation taxa can inform our understanding of adaptation and speciation, as well as broader environmental management and restoration strategies.

Among plants in high-mountain regions, trees are particularly interesting for studying genetic adaptation. For example, due to their long lifespan, it is possible to combine their individual multiyear responses to environmental factors with genomic data by jointly analysing individual tree rings and genetic variation (so-called dendrogenomics, Heer et al. 2018; Housset et al. 2018; Krutovsky 2022). Moreover, mountain trees growing in heterogeneous landscapes along altitudinal gradients are particularly suited for studying plant adaptation to abiotic stress under extreme conditions (e.g., Schrieber et al. 2020). Investigating their genetic adaptation mechanisms requires integrated multidisciplinary approaches by combining analyses of phenotypic variation with genomics or even multiomics approaches that also include transcriptomics, proteomics, metabolomics, epigenomics, etc. (Bräutigam et al. 2013; Voelckel et al. 2017; Rodrigues et al. 2021; Borthakur et al. 2022; Sarath et al. 2024).

Alpine forest genomics studies how tree species and associated organisms have evolved in and will adapt to heterogeneous mountain landscapes and ongoing climate change (Neale et al. 2013). Although the term contains

“alpine,” the research conducted mainly includes mountainous, subalpine regions where trees frequently occur. It is a relatively new, rapidly developing and important research field that uses genomic tools and techniques to study mainly (but not only) genetic diversity, gene flow, demographic history and genetic adaptation and evolution of primarily trees and shrubs, and their associated organisms, in subalpine forest ecosystems. Over the past two decades, rapid advances in high-throughput sequencing, with its short- and long-read sequencing technologies, have massively transformed the field and facilitated forest genomics research (Plomion et al. 2016; Isabel et al. 2020; Borthakur et al. 2022). Researchers have successfully applied different evolutionary, population and landscape genomic tools and approaches to study subalpine forest tree species such as Norway spruce (*Picea abies* (L.) H. Karst.) (Mosca et al. 2018; Zhou et al. 2024; Avanzi et al. 2025), Swiss stone pine (*Pinus cembra* L.) (Rellstab et al. 2019; Dauphin et al. 2020, 2021; Gugerli et al. 2023), Siberian stone pine (*Pinus sibirica* Du Tour) (Novikova et al. 2024), dwarf mountain pine (*Pinus mugo* Turra) (Mosca et al. 2012, 2016), Scots pine (*Pinus sylvestris* L.) (Köbölkuti et al. 2020), silver fir (*Abies alba* Mill.) (Mosca et al. 2014; Behringer et al. 2015; Heer et al. 2018; Csilléry et al. 2020; Pélachs et al. 2026), European larch (*Larix decidua* Mill.) (King et al. 2013; Gömöry et al. 2015), and Siberian larch (*Larix sibirica* Ledeb.) (Novikova et al. 2023, 2026). In addition, the community has contributed to sequence, assemble and annotate some of the first conifer whole chloroplast, mitochondrial and nuclear genomes of whitebark stone pine (*Pinus albicaulis* Engelm.) (Neale et al. 2024), *A. alba* (Mosca et al. 2019; Kersten et al. 2022), and *L. sibirica* (Bondar et al. 2019; Kuzmin et al. 2019; Putintseva et al. 2020). By studying the complete genomes of these organisms, alpine forest genomics helps uncover the molecular basis of resilience and adaptation, contributing valuable tools and insights for the conservation of these fragile ecosystems.

A literature review about alpine forest genomics was lacking so far. Here, we therefore carried out a systematic bibliometric analysis focusing on seven important European conifer species growing in high elevations to describe past and current research in alpine forest genomics. We complemented this review by a survey of members of the Alpine Forest Genomics Network (AForGeN, IUFRO Working Party 2.04.11) to identify research challenges they are currently facing and to

reveal upcoming research topics in the field. AForGeN was founded in 2012 by researchers led by David Neale (Neale et al. 2013, Table 1) and held its 11th meeting in Todtmoos (Black Forest), Germany, during June 2026 (<https://aforngen.org>). By combining these two approaches, we aimed at identifying the past and current trends in the research field, as well as limitations, challenges and perspectives for the future.

2 Methods

2.1 Alpine forest genomics research over the years 2000–2024

2.1.1 Methodology of the bibliometric analysis

We conducted a systematic literature search in Web of Science™ (WOS, Clarivate™) in January 2025 for publications from the years 2000–2024 including the following search terms in title, abstract or keywords: *Pinus cembra*, *Pinus mugo*, *Pinus sibirica*, *Larix decidua*, *Larix sibirica*, *Abies alba*, *Picea abies*, genom* and genet* (for further details see Appendix 6.; Budde et al. 2026). A preliminary search using the terms “tree” or “forest” and “mountain” or “alpine” and “genom*” or “genet*” retrieved very few targeted publications and missed many publications which we considered important for this research field. The included conifers share key traits characteristic of alpine and montane forests: they are long-lived, dominant canopy species that provide much of the structural framework and economic value of mountain forests across broad elevation gradients. In contrast, e.g., *Betula pendula* Roth and *Alnus viridis* (Chaix) DC. generally occupy complementary but more peripheral ecological roles, primarily as pioneer or shrub-layer species, and therefore do not define the structure and functioning of the alpine forest biome to the same extent

(San-Miguel-Ayanz et al. 2016). As such, our literature analysis described here represents a case study involving only European, high-elevation and coniferous tree species and does not claim completeness or a global representation of the field. For comparison, public articles including AForGeN members in the authorship were retrieved from the network’s website (<https://aforngen.org>) using the stringr package (Wickham 2010) in R v4.3.3 (R Core Team 2024) and filtered for publications involving the target species.

We performed manual filtering on the full list of references by removing publications which did not directly study the target species or focused mainly on other organisms such as associated pests and pathogens. We also excluded publications about the development and optimization of in vitro culture techniques. On this filtered publication list, we conducted the bibliometric analysis. First, we explored the development of yearly publications from 2000 to 2024 and compared the total publication output including publications from AForGeN members.

As analyses of keywords suffer from synonyms and a non-consistent assignment by authors (Lu et al. 2020; Sampagnaro 2023), we decided to perform a topic model analysis (Blei et al. 2003; Griffiths and Steyvers 2004; Hofmann 2017) on the combination of titles, author keywords and abstracts. In particular, abstracts bear more semantic knowledge (Chen et al. 2024). For doing so, we used the frequency of bi-grams (pairs of words) in the abstract, keywords and title of each publication. In order to avoid topics of limited importance, it was stipulated that each bi-gram must occur in at least 10 publications. We also removed certain terms which formed very general bi-grams, like “significant correlation” or “two species” as they were not topic-specific but could appear in

Table 1 The origin of the Alpine Forest Genomics Network (AForGeN) by David B. Neale

During the early 2010s, I had the opportunity to lead a multi-investigator and multi-institutional project in Trentino, Italy, called Alpine Ecosystems in a Changing Environment (ACE-SAP). My individual contribution to this project was to conduct landscape genomics research for several conifer species found in the mountainous regions of Trentino. Elena Mosca joined my lab at UC Davis as a postdoc and conducted landscape genomics studies in *A. alba*, *P. abies*, *P. cembra*, *P. mugo*, and *L. decidua*. All of these studies were done prior to having complete genome sequences for these species, so SNPs were discovered by resequencing candidate genes and large numbers of expressed sequence tags (ESTs). When the ACE-SAP project was completed, I had the opportunity to continue this line of research at the Istituto Agrario di San Michele all’Adige (IASMA, now the Foundation Edmund Mach). Before designing the next generation of research in mountain forest conifers, I decided to learn more about similar research being conducted in other European countries. To that end, I visited with Felix Gugerli in Zürich, Berthold Heinze in Vienna and Beppe Vendramin in Florence. I had some familiarity with genomics research in mountain forest trees in Europe but these researchers made me aware of many more researchers in Germany, Slovenia, France, Slovakia, Hungary, and more. What stood out to me immediately was that nearly everyone was asking the same questions, in the same species, and were using very similar approaches. What differed in many, but not all cases, was that sampling was constrained to domestic boundaries, sometimes due to funding constraints. My next thought was simply “Why don’t we find a way to work together in a coordinated and cooperative manner?”. Were the community of mountain forest genomics researchers in Europe able to find a platform to do this, then gaps and redundancies could be identified and harness the intellectual creativity and energy that can result from large cooperative/collaborative projects. Similar projects often are created in a top-down manner from funding agency initiatives. Given that no such initiative was under consideration, my thought was to develop something from the bottom up. I then proposed this idea to the students and postdocs at IASMA who were working in forest genomics. After a several hour brainstorming session, together we came up with the name Alpine Forest Genomics Network (AForGeN) and planned an initial meeting in the Adamello Brenta, Italy, for June 2012. Invitations were sent to everyone in Europe we knew and announced that the meeting would be open to anyone interested in this topic and joining a network. And so AForGeN was born, shortly after became an IUFRO working party (2.04.11) and continues today due to the passion and cooperative spirit of its members.

thematically very different publications. We weighted the resulting bi-grams with respect to the collection frequency (Term Frequency-Inverse Document Frequency, Sparck Jones 1972), i.e., matches on less frequent, more specific, terms obtain greater values. Based on the resulting document–bi-gram matrix, we conducted a clustering analysis using non-negative matrix factorization (Lee and Seung 1999) as implemented in the Python 3.13 (Van Rossum and Drake 2009) library scikit-learn (Pedregosa et al. 2011). We used normalized pointwise mutual information (NPMI, Lau et al. 2014) as a metric to evaluate the quality of the resulting topic model. To interpret the topic clusters, we plotted the importance of the first seven bi-grams for each topic and assigned a category name to each topic (7. Figs. 6 and 7). We used topic models with both 8 and 17 topics, showing similarly high NPMI values (see Sect. 3), to analyze the field at different scales of resolution. The 8-topic model was used to identify broad research categories (macro-perspective), while the 17-topic model was employed to distinguish between more nuanced and closely related research topics (micro-perspective), such as separating population genetics from adaptation genomics (see Sect. 3). Based on these topic models we explored temporal trends in publication frequency over the 25-year study period. Each publication was assigned a main research topic based on the topic models and we plotted the publication share per topic per year.

Topic information was extracted from the Descriptor (DE) field of the Web of Science output, modified as follows: prior to network construction, the keywords in the DE field were replaced with the three most important topics as identified by the topic models with 8 and 17 topics, respectively. A co-occurrence network incorporating the temporal dynamics of the predefined topics was constructed to illustrate their evolving relationships over time for both topic models. Data manipulation and analysis were performed using the readr (Wickham et al. 2026), tidyverse (De Brouwer 2020), and dplyr (Wickham et al. 2023) R-packages. Visualizations were generated with ggplot2 (Wickham 2011). Co-occurrence network analyses were conducted with VOSviewer (Van Eck and Waltman 2010). The nodes represent the predefined topics, while the edges represent the co-occurrences of these topics. The strength of the co-occurrence relationship of topics was given by the normalized association strength calculated by VOSviewer, which also considers the absolute frequency of occurrence of each element. Clustering was performed using the VOS clustering technique (Waltman et al. 2010), which employs a weighted and parameterized variant of modularity-based clustering. The visualization of the co-occurrence networks was produced using the VOS layout algorithm, which places

elements in two dimensions based on similarity values, so that similar elements are closer to each other and less related elements are further apart. Co-occurrence network final figures were edited and formatted in Inkscape (Inkscape Project 2023).

2.2 Survey on research perspectives and challenges in the past and future

In December 2024, we reached out to all 93 AForGeN members with a questionnaire regarding the research perspectives in alpine forest genomics and the expected challenges in the coming decade. The questions were kept broad and open on purpose; no predefined selection for answers was given. This allowed the participants to give unbiased answers.

The following six questions were included in the questionnaire:

- 1) What will be the three main research topics in the research field of alpine forest genomics in the future?
- 2) What would you study in alpine forest genomics if there were no constraints?
- 3) Where do you see the main challenges/constraints regarding these research topics in the future?
- 4) What is missing so far in terms of resources in alpine forest genomics research?
- 5) How could AForGeN contribute to achieving the goals you listed in question 1 and overcoming the challenges you listed in question 3?
- 6) From the researcher's perspective, what and how can the field of alpine forest genomics contribute to applied activities like forest management or nature conservation?

For each question, a maximum of three answers were allowed. We created a map illustrating the institutional locations of the scientists who answered the survey using the R-package rnatuarearth v1.1.0 (Massicotte and South 2026) and a word cloud of all answers with <https://wordart.com/>. The answers were then grouped into broader categories independently by two authors. Categories were subsequently cross-checked and their names synchronized. Agreement in categories was very high. For example, in question 1, they differed by only one category.

3 Results

3.1 Trends in publication outputs

The literature search yielded a total of 869 publications, and 662 publications were retained after manual filtering for the bibliometric analysis. The yearly number of publications declined between 2002 and 2006, followed by a peak around 2008 (25 publications) and an upward trend between 2009 (16 publications) and 2019 (50

publications, [Appendix Fig. 4](#)). Since the foundation in 2012, the contribution of the AForGeN members oscillated between 15 and 31% of overall publications. *Picea abies* was the most studied species over the whole time period with a total of 388 (59%) publications followed by *A. alba* (121 publications, 18%) and *L. decidua* (61 publications, 9%).

3.2 Research topics in alpine forest genetics and genomics

The quality metric NPMI indicated the highest coherence for topic models with 8 and 17 topics, respectively ([Appendix Fig. 5](#)). The seven most important bi-grams of each topic were plotted to characterize and categorize the topics. The following research topics were identified by the model comprising eight topics: *genetic diversity*, *quantitative genetics*, *seed orchards*, *genetic structure*, *climate response*, *wood properties*, *environmental adaptation*, and

genome structure ([Appendix Fig. 6](#)). These broad topics could be further split and revealed narrower research topics in the model with 17 topics: *genetic diversity*, *genetic correlations*, *seed orchards*, *genetic trait variation*, *climate change*, *wood properties*, *environmental adaptation*, *organelle genome structure*, *breeding*, *gene expression*, *genetic structure*, *nuclear genome structure*, *genetic differentiation*, *growth*, *gene flow*, *disease resistance*, and *dendroecology* ([Appendix Fig. 7](#)). To explore the temporal dynamics of the 8 and 17 topics, respectively, within the broader field of alpine forest genomics with a focus on the seven conifer species, trends in publication frequency over time and per topic were visualized (Fig. 1, [Appendix Fig. 10](#)). While the proportion of publications about quantitative genetics and genetic structure was especially high in the years 2000 to 2010, publications about climate responses and environmental adaptation became more frequent in recent years.

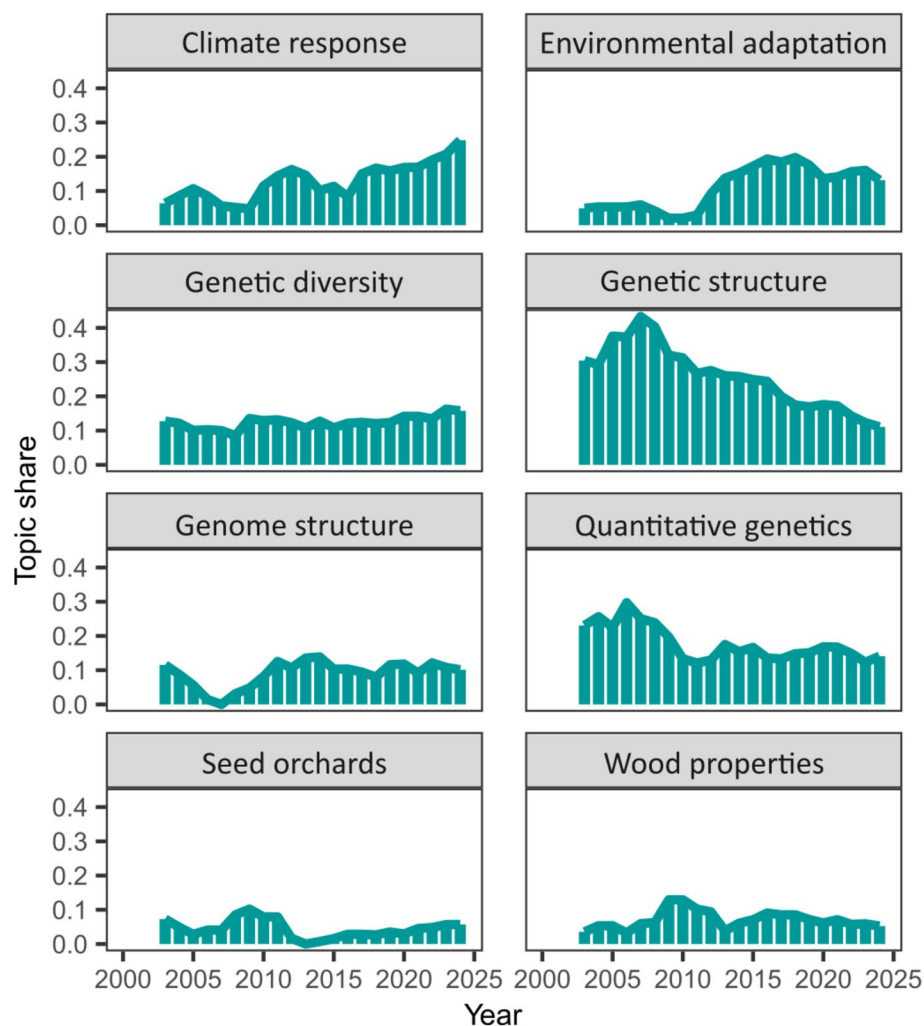


Fig. 1 Publication share trends smoothed over intervals of 4 years for each of eight research topics. These topics were identified in the 662 publications in alpine forest genetics/genomics of seven European conifer species published between 2000 and 2024

The co-occurrence network (Fig. 2) revealed that alpine forest genomics research, across the eight identified topics, is structured into two distinct scientific clusters: the red cluster comprising *genetic structure*, *genetic diversity*, *seed orchards*, *climate response*, and *quantitative genetics*, which can be described as population genetics, and the green cluster including *environmental adaptation*, *genome structure*, and *wood properties*, which relates to functional genomics. Among these, *genetic structure* (51%) and *environmental adaptation* (45%) emerged as the two most dominant topics, reflecting their central role in alpine forest genomics research.

In the co-occurrence network comprising 17 topics (Appendix Fig. 11), three distinct scientific clusters were identified: the red cluster comprising *organellar genome structure*, *nuclear genome structure*, *disease resistance*, *environmental adaptation*, and *dendroecology*, the green cluster—*climate change*, *wood properties*, *genetic correlations*, *growth*, *breeding*, and *seed orchards*, and the blue cluster—*gene flow*, *genetic differentiation*, *genetic structure*, *genetic diversity*, and *genetic trait variation*. Among them, the topics *genetic differentiation* (32%) and *genetic trait variation* (26%) emerged as the two most common topics. Interestingly, *genetic trait variation* showed only limited association with *breeding* in the co-occurrence network. This observation suggests that research on trait variation in alpine conifers remains largely focused on evolutionary ecology and natural populations, with fewer

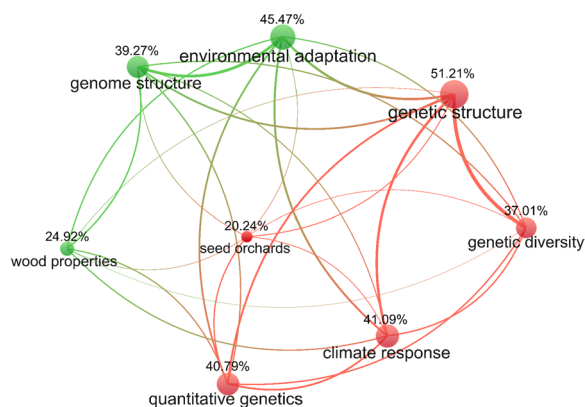


Fig. 2 Co-occurrence network of the eight main research topics in the alpine forest genomics literature of seven European conifer species over the 25-year period (2000–2024). The spatial proximity of circles reflects the relative strength of association and thematic similarity between topics. Topics within the same cluster are indicated in green (functional genomics) and red (population genetics). Font size and node size correspond to the number of publications in which each topic appears, while connecting lines represent co-occurrence relationships; the thickness of each line denotes the frequency with which two topics co-occur in the same publications. The percentages shown above each node illustrate that topic's proportion of occurrence across all publications

direct links to applied breeding efforts, highlighting a potential gap in the integration of adaptive genetics into forest management.

We also examined the temporal publication trends of the eight main research topics during the 25-year period for *P. abies*, the most studied species (Appendix Fig. 8), and the other species (Appendix Fig. 9) separately. The highly similar patterns in topic shares observed in publications about *P. abies* and all publications indicate how strongly this species impacts the overall topic trends, which was to be expected given the dominance (59%) of Norway spruce in the retained set of publications. *Genetic diversity* and *genetic structure* dominated in almost all species, especially *A. alba*, *L. decidua*, and *P. abies*. For *P. sibirica* and *P. cembra*, the number of publications was low with only 27 and 31 publications, respectively, and publications are more aggregated in time. For *P. mugo* and *L. sibirica*, research activity has increased starting from 2010. The *climate response* and *environmental adaptation* topics are present in almost all species, showing an increase in recent years, which may indicate a strengthening of research priorities related to climate change.

The most cited publications (all with number of citations above 100) mainly focused on *P. abies* (13 out of 18, 72%), which again emphasized the role of *P. abies* as model species in alpine forest conifer genetics. The most cited publication by far described the nuclear reference genome of *P. abies* (Nystedt et al. 2013), which was the first ever published conifer reference genome assembly (Table 2).

3.3 Survey on research perspectives and challenges in the past and future

We received a total of 25 answers of the 93 contacted AForGeN members (27%). The word cloud already indicated some of the main research topics of AForGeN members, i.e., genomes, adaptation, and forests (Appendix Fig. 12).

The answers to question 1 strikingly showed that the members of AForGeN consider adaptation genomics as the primary research topic of the future (Fig. 3); 92% of responding members mentioned this or a related keyword. After that, the establishment of genomic resources, the study of elevational and range shifts, and assisted migration/gene flow were the most prominent topics. The interest in adaptation genomics was confirmed by question 2, where members could indicate what they would personally choose to study if there were no constraints (Fig. 3). This was followed by the intention to do more experimental work and put emphasis on genomic resources, biotic interactions, and structural variants in the genome. Interestingly, some assumed future hot

Table 2 Genomic resources of mountainous conifer species

When AForGeN was started, reference genome assemblies of conifers were still missing. In particular, the large genome sizes and high repeat contents (primarily due to transposable elements, TEs) of conifer species makes the generation of reference genomes challenging and costly. First, there were efforts in producing transcriptomic sequences in various species (e.g., Lorenz et al. 2006; Parchman et al. 2010), but not yet as comprehensively (from different tissue/cell types, life stages and individuals) as would be desirable. The first conifer draft genome that was published (Norway spruce, *P. abies*; Nystedt et al. 2013) was highly fragmented and incomplete. Also, resources in terms of ready-to-use large marker/SNP assays were rare (but see e.g., Chen et al. 2012; Eckert et al. 2010a; Eckert et al. 2009; Eckert, van Heerwaarden, et al. 2010b). The AForGeN therefore discussed the possibility of generating such resources and decided to establish an *A. alba* reference assembly as a first, community-funded effort (Mosca et al. 2019), from which later further genomic resources like SNP chips or probes for targeted sequencing could be developed (Pinosio et al. 2026). In recent years, the availability of genomic resources has substantially improved, also in conifer species (7. Tables 3 and 4). For example, new high-quality reference assemblies of *P. sylvestris* and *P. abies* at the chromosome level were created recently (Nilsson et al. 2025). Long-read and Hi-C sequencing have enabled substantially improved assemblies and annotation (Neale et al. 2024), making the production of haplotype-resolved assemblies possible (An et al. 2022). However, the annotation of these immense and highly complex genomes is still limited. Species with high-quality genomic resources attract more attention from scientists, leading to further projects, insights, publications (Ellegren 2014) and breeding initiatives. Thus, there is a need to further produce high-quality references genome assemblies and other genomic resources for further ecologically important mountainous conifer tree species (e.g., *P. mugo*, *P. cembra* or *L. decidua*; 7. Table 3). Additionally, some useful resources such as SNP arrays or probes designed for targeted sequencing/genotyping were developed with commercial companies, and are not always openly available (but see, e.g., Pinosio et al. 2026).

Several initiatives aim at producing new or improved genome assemblies which are currently under development, such as for *A. alba* (AForGeN), *P. sylvestris* and *P. abies* (Nilsson et al. 2025), and *P. sibirica* (Konstantin Krutovsky, personal communication). Pangenome initiatives which will facilitate the analyses of structural variants, i.e., insertions, deletions, inversions, copy number and gene presence/absence (Fang and Edwards 2026), are underway for broad-leaved species with considerably smaller genomes (e.g., Liang et al. 2025; Wood et al. 2025) but are also expected to develop for conifer species in the coming years.

topics (question 1) were (almost) not considered for own research by AForGeN members, e.g., assisted migration/gene flow, genetic diversity, and range/elevation shifts. Vice versa, topics like reproduction, hybridization, and phenotypic variation seemed to be interesting for the network members, but were not considered as topics of general importance.

Question 3 and 4 dealt with challenges, constraints and missing resources in alpine forest genomics. Financial, genomic, and experimental resources were considered as the main constraints in performing the research that was planned (Fig. 3), followed by missing know-how (also on tree biology) and sampling constraints, mainly due to the difficult territory. This was confirmed by question 4, where again genomic, experimental, and financial resources were mentioned as frequently missing (Fig. 3), although in a different ranking than in question 3. Here, the answers also showed that data or even general knowledge about environment, phenotypes, and gene functions are also missing.

In question 5, we asked about the potential role of AForGeN in performing the research listed in question 1 and in the challenges mentioned in question 3. The answers showed that the value of the network was mainly seen in its collaborative efforts, be it enabling straightforward collaboration, applying for joint projects or coordinating activities among the institutes. Interestingly, the development of genomic resources was not mentioned here, but may be included in the joint projects. Finally, question 6 dealt with the applied benefit of alpine forest genomic research. About half of the members indicated that insights from the research field could help to guide

forest management strategies. This, followed by the goal to convince practice that adaptive genomic diversity is an important part of genetic diversity, needs to be increasingly addressed, and the identification of future genetic conservation units (GCUs). In Europe, GCUs are officially recognized areas at the national level intended to conserve the genetic diversity and evolutionary potential of a targeted tree population in situ. The populations must meet a minimum size requirement, and management measures and silvicultural techniques may be applied to support genetic processes within the target tree populations as defined by EUFORGEN (European Forest Genetic Resources Programme; Koskela et al. 2013).

4 Discussion

4.1 Availability of genomic resources boosts further research

Well-characterized species with available genomic resources tend to attract further projects and funding, which in turn generate new results, a pattern widely observed in model organism research (Ellegren 2014). This finding was exemplified by the economically important *P. abies*, which was identified as the most studied species in our bibliometric analysis and for which the first conifer reference genome had been developed (Nystedt et al. 2013). Less economically important tree species, such as *P. cembra* and *P. mugo*, remain underrepresented in genomic research, despite their ecological importance in mountain ecosystems, suggesting that research priorities are driven more by economic importance than by ecological relevance (Neale and Kremer 2011).

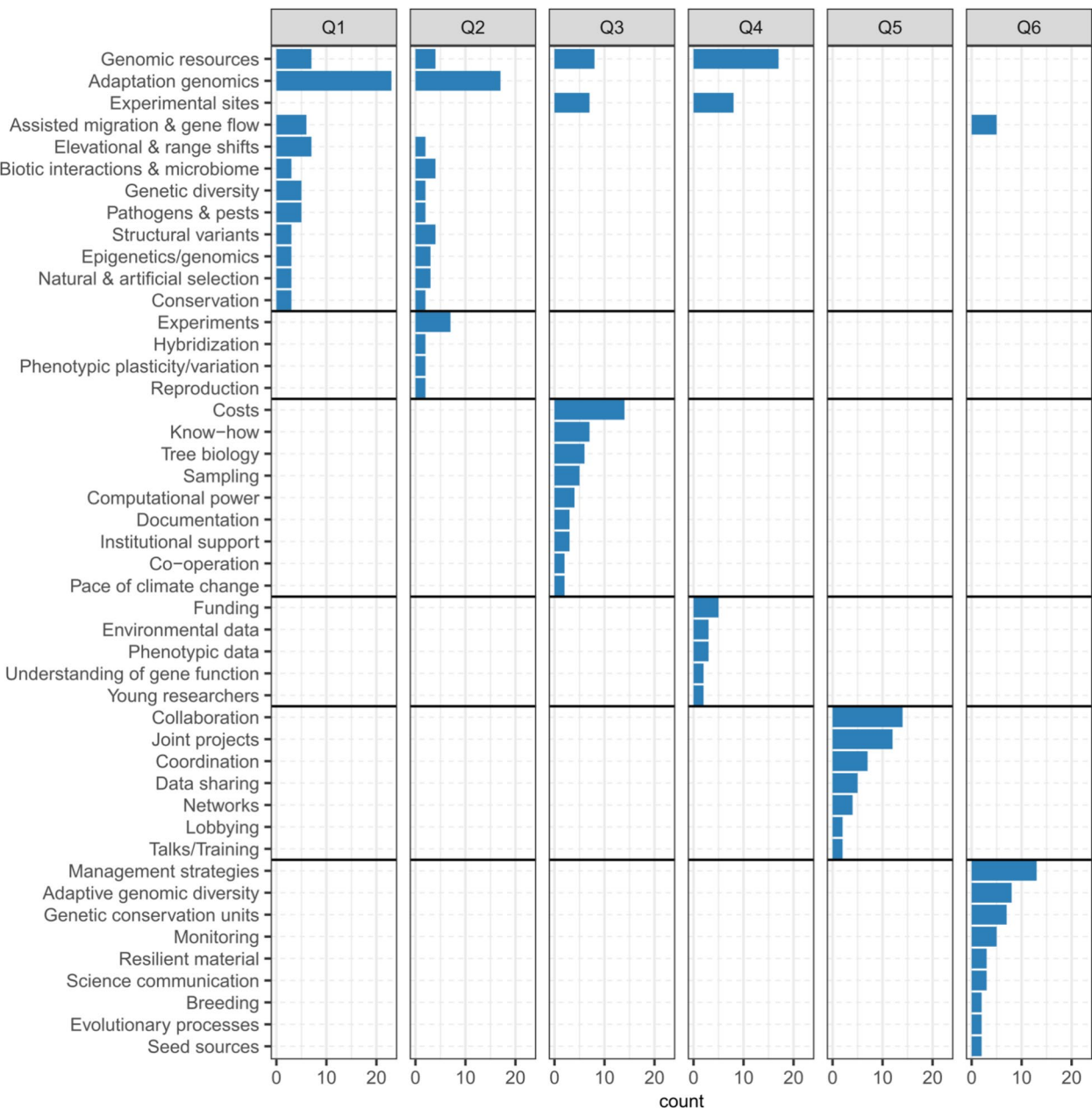


Fig. 3 Answers of the members' survey on future research topics (Q1: main future research topics, Q2: own future research without constraints), challenges and constraints (Q3), missing resources (Q4), the role of AForGeN (Q5), and applied contributions of the research field (Q6). Topics and keywords with only one answer are not shown. If possible, categories were applied across the different questions

4.2 Climate adaptation genomics is the hot topic – now and in the future

Adaptation genomics was viewed by far as the most important research topic in the AForGeN member survey and also showed an increase of research output over the last 20 years in the bibliometric analyses (*environmental adaptation* and *climate response*, Fig. 1). This topic is particularly urgent due to rapid environmental

change caused by global climate change, but also global trade and movement of species introducing novel pests and pathogens. Understanding adaptive processes demands a genome-level understanding of how species may cope with, adapt to and persist under these newly arising selective pressures. Genotype–environment associations can reveal signatures of environmental selection and adaptation (Rellstab et al. 2015), but also enable the

detection of maladaptation risks under climate change scenarios (Capblancq et al. 2020; Rellstab et al. 2021; Novikova et al. 2026). Furthermore, genotype–phenotype association studies can identify loci that potentially control trait variation, thereby facilitating genomic selection e.g., based on target loci for adaptive traits within breeding programmes (Neale and Kremer 2011). Therefore, genomic insights are key to developing suitable conservation and management strategies of tree populations that can survive extreme drought and heat periods or attacks by pests and pathogens. As many populations are expected to face maladaptation, also assisted migration and gene flow were considered as important research topics which deserve attention especially in the highly fragmented, mountainous forest landscape in Europe.

Topics like genetic differentiation and genetic structure showed a declining temporal trend in the bibliometric analysis. While these topics remain important, this might indicate that baseline characterizations have already been established for many species and regions. Consequently, they are now less frequently the primary focus of new studies. Instead, they are routinely incorporated as important background knowledge or underlying variables—for example, accounting for population genetic structure is a standard prerequisite when conducting genome scans.

The availability of genomic resources, in particular for conifer species with large genome sizes, is still limited. However, sequencing technologies are advancing quickly and respective costs are decreasing. Therefore, and as indicated by the research plans of AForGeN members in our survey, more genomic resources are expected to become available soon that will enable further genomic research in non-model tree species. Expertise from different disciplines, such as genomics, ecology, evolution, forest sciences, dendrochronology, climatology, and bioinformatics is needed to address these research topics, ideal for a collaborative research network like AForGeN.

4.3 Interdisciplinary research, such as dendrogeonomics, is key to address pressing research questions

The bibliometric analyses—although specifically addressing genetic and genomic studies—brought up several topics not directly linked to molecular genomics, like quantitative genetics and wood properties (in the 8 topics model), and seed orchards, breeding, trait variation, growth, disease resistance or dendroecology (additionally in the extended 17 topics model). This outcome shows that interdisciplinary approaches are needed to address

evolutionary and plastic responses related to stressors like climate change, pathogens or land-use changes. A prime example of such interdisciplinary work is the research field of dendrogeonomics (Krutovsky 2022) that links genomic information of individual trees to retrospective functional traits related to, e.g., annual growth, extreme climatic events or water-use efficiency. Stimulated by the pioneering work of Heer et al. (2018) and Housset et al. (2018), this interdisciplinary field has gained importance (e.g., Trujillo-Moya et al. 2018; Baison et al. 2019; Depardieu et al. 2021; Martínez-Sancho et al. 2021; Novikova et al. 2024; Pålsson et al. 2026), especially when studying climate responses of trees. Other promising interdisciplinary works include common garden experiments (De Villemereuil et al. 2016), stable isotopes (in leaves/needles or tree rings, Gessler et al. 2014) or disease resistance (e.g., Singh et al. 2024; Stocks et al. 2019). In contrast, the AForGeN member survey did not reveal a substantial present or planned focus on interdisciplinary topics. This might reflect that AForGeN mainly consists of researchers from the field of population genetics who acknowledge the benefit of interdisciplinary approaches (e.g., Heer et al. 2018; Krutovsky 2022) but are challenged by the difficulty to collect trait-related datasets in mountainous territory (e.g., in experiments, see below). An important venue could be future collaborations with ecophysiologicalists to disentangle the relative contributions of genetic adaptation and phenotypic plasticity to tree survival (as in e.g., Martínez-Sancho et al. 2025 and Pålsson et al. 2026 using wood core traits). Such interdisciplinary efforts, potentially also incorporating epigenetic analyses, would provide a more holistic understanding of how mountainous tree species respond to rapid climate shifts, distinguishing between genetic traits and flexible physiological responses.

4.4 Genomic, financial and experimental resources represent the main challenges in alpine forest genomics research

The AForGeN member survey, based on a rather limited number of participants, revealed three main challenges related to planned science in the future: availability of genomic resources, costs/funding, and experimental sites. The first challenge, scarce genomic resources, is mostly related to the large size and repetitive nature of conifer genomes (as discussed in Table 2), leading to either a lack of or highly fragmented reference assemblies (Nystedt et al. 2013; Mosca et al. 2019). But even if such high-quality resources exist, individual whole-genome

re-sequencing is still costly for species with huge genome sizes (second challenge), especially for population genetic and adaptation genomic studies that require large sample sizes. Therefore, alternative approaches, such as reduced representation (e.g., ddRAD, targeted sequencing, targeted capture sequencing or single primer enrichment technology [SPET]), low-coverage or pooled-sequencing, and single-nucleotide polymorphism (SNP) panels (or their combination) have been or are still widely used in the target species. Most of these approaches, however, again benefit from or require high-quality reference genome assemblies. The recent advances in long-read sequencing will hopefully boost the establishment of reference genome assemblies also for conifer species (Neale et al. 2022, 2024). The AForGeN is currently collaborating on an improved version of the *A. alba* reference assembly. Moreover, several large collaborative projects, funded by the European Union, like GenTree (www.gentree.eu, targeted capture sequencing) and FORGENIUS (www.forgenius.eu, SPET) have created probes or SNP panels that are publicly accessible and can be used for various purposes (Milesi et al. 2024; Francisco et al. 2025; Pinosio et al. 2026). Additionally, multi-species, multi-site common gardens are currently being planted in several European countries in the framework of the OptFORESTS project (www.opforests.eu) and a database of existing common gardens for various forest tree species is currently under construction in the same project. An alpine-type common garden comprising among others *A. alba* and *L. decidua* will be planted in four locations, two in the Alps, one in the Pyrenees, and one in the Czech Republic. We expect that these new genomic resources and common garden sites will stimulate research amongst others into mountainous conifer species in the coming years.

5 Conclusion

Our analyses revealed that alpine forest genomics has transitioned from classic population genetics towards environmental adaptation genomics, driven largely by

the availability of genomic resources, in particular for *P. abies*, and the acceleration of climate change. While adaptation genomics is recognized as the primary research direction for ensuring climate-resilient forest management, significant bottlenecks remain regarding funding, experimental infrastructure, and genomic resources for non-model species.

To overcome these constraints and advance from associations between genomic, phenotypic and environmental data towards functional understanding of adaptation, future research should adopt a more interdisciplinary approach. Specifically, there is an urgent need for integrated ecophysiological studies to validate the functional understanding of putatively adaptive traits and epigenetic studies to uncover the role of phenotypic plasticity in long-lived conifers. By combining these approaches with additional genomic resources, the field can improve the necessary scientific basis for the conservation and sustainable management of vulnerable mountainous forest ecosystems in the face of rapid climate change.

Appendix

Web of Science literature search

The following terms were searched in title, abstract, and keywords to retrieve publications from the Web of Science (Clarivate™):

PY=(2000-2024)

AND

((AB=("Pinus cembra" OR "Pinus mugo" OR "Pinus sibirica" OR "Larix decidua" OR "Larix sibirica" OR "Abies alba" OR "Picea abies") OR TI=("Pinus cembra" OR "Pinus mugo" OR "Pinus sibirica" OR "Larix decidua" OR "Larix sibirica" OR "Abies alba" OR "Picea abies") OR AK=("Pinus cembra" OR "Pinus mugo" OR "Pinus sibirica" OR "Larix decidua" OR "Larix sibirica" OR "Abies alba" OR "Picea abies"))

AND

((AB=(genom* OR genet*) OR TI=(genom* OR genet*) OR AK=(genom* OR genet*))

Publication trends

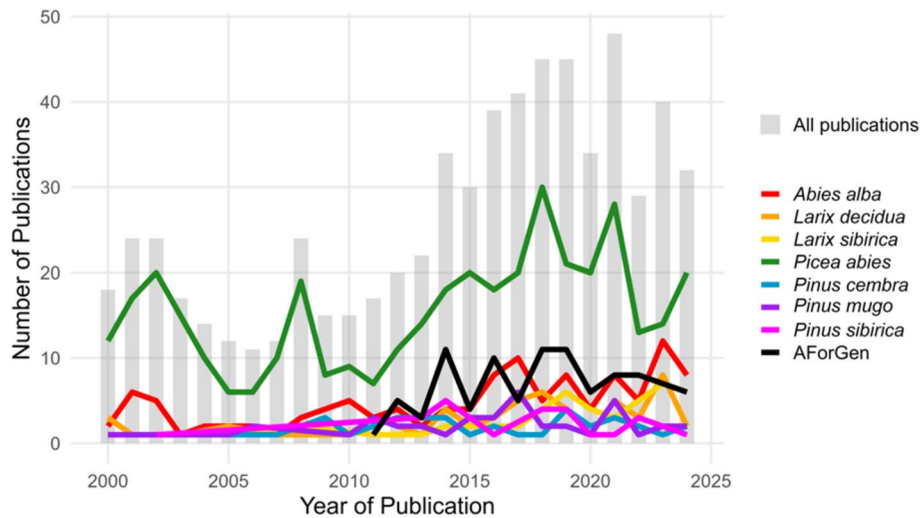


Fig. 4 Publication trends (2000–2024) for the selected conifer species and the respective contribution of AForGeN members. Gray bars represent the total number of publications per year over all species. Colored lines show species-specific trends, while the black line represents publications authored by AForGeN members

Topic models and average NPMI as coherence measure of the topic models

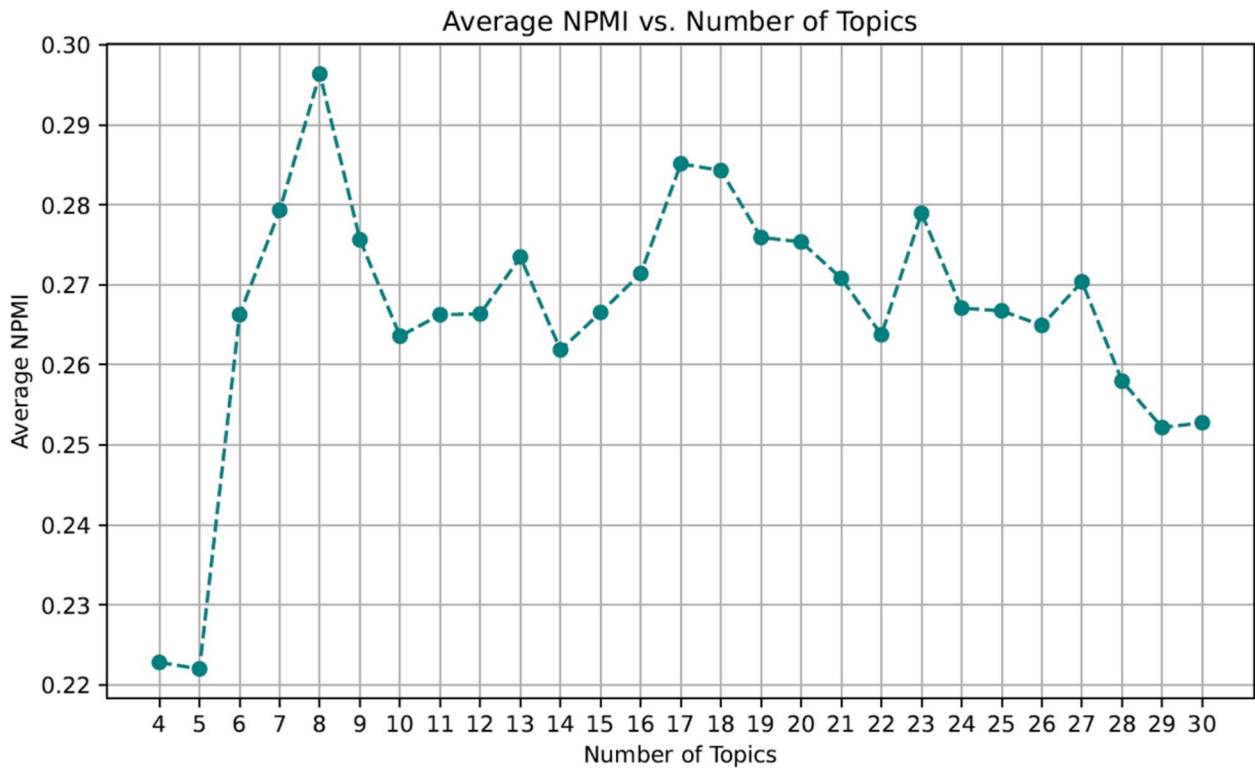


Fig. 5 The average NPMI values for topic models identified for the 662 publications included in the bibliometric analyses. Peaks for topic models comprising 8 and 17 topics respectively indicate high coherence.

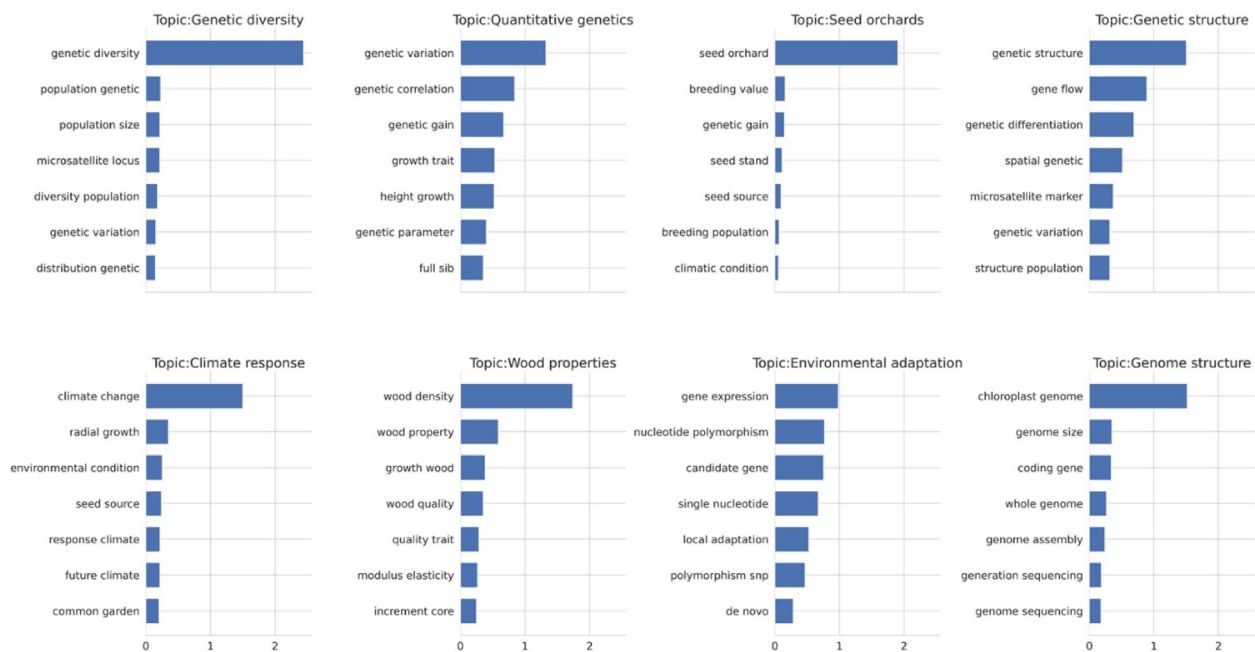


Fig. 6 Topic model with eight topics identified based on the co-occurrence of pairs of words in abstract and title of 662 publications. The topic titles were assigned by the authors based on the word pairs with high priority in each topic.

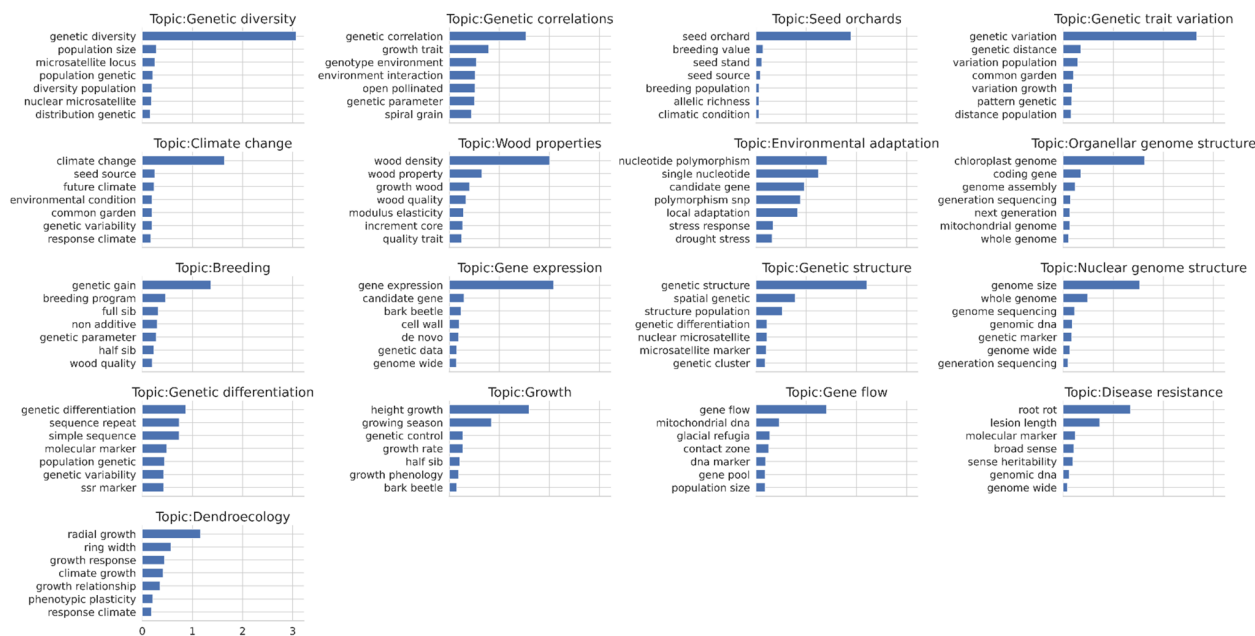


Fig. 7 Topic model with 17 topics identified based on the co-occurrence of pairs of words in abstract and title of 662 publications. The topic titles were assigned by the authors based on the seven word pairs with highest priority in each topic.

Temporal trends of topics in alpine forest genetics and genomics

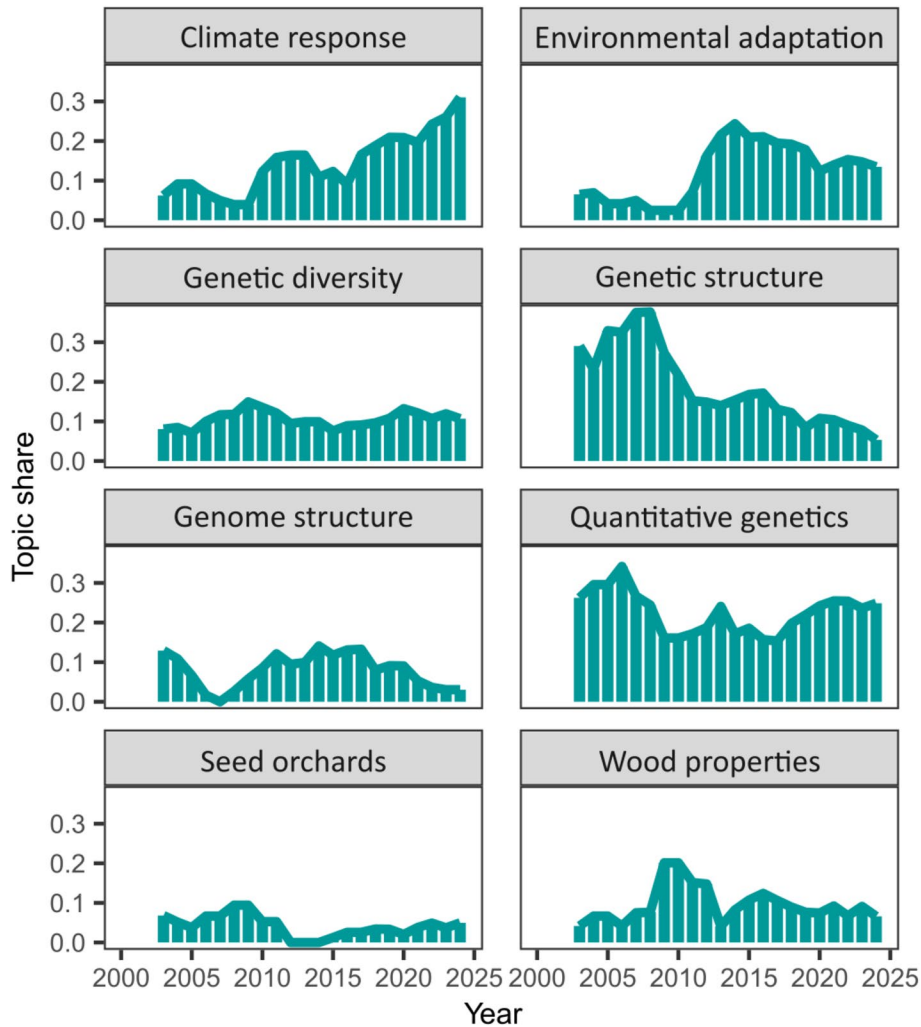


Fig. 8 Publication share trends smoothed over 4-year intervals for each of eight research topics in publications studying *Picea abies* published between 2000 and 2024. For all other species, see Appendix Fig. 11

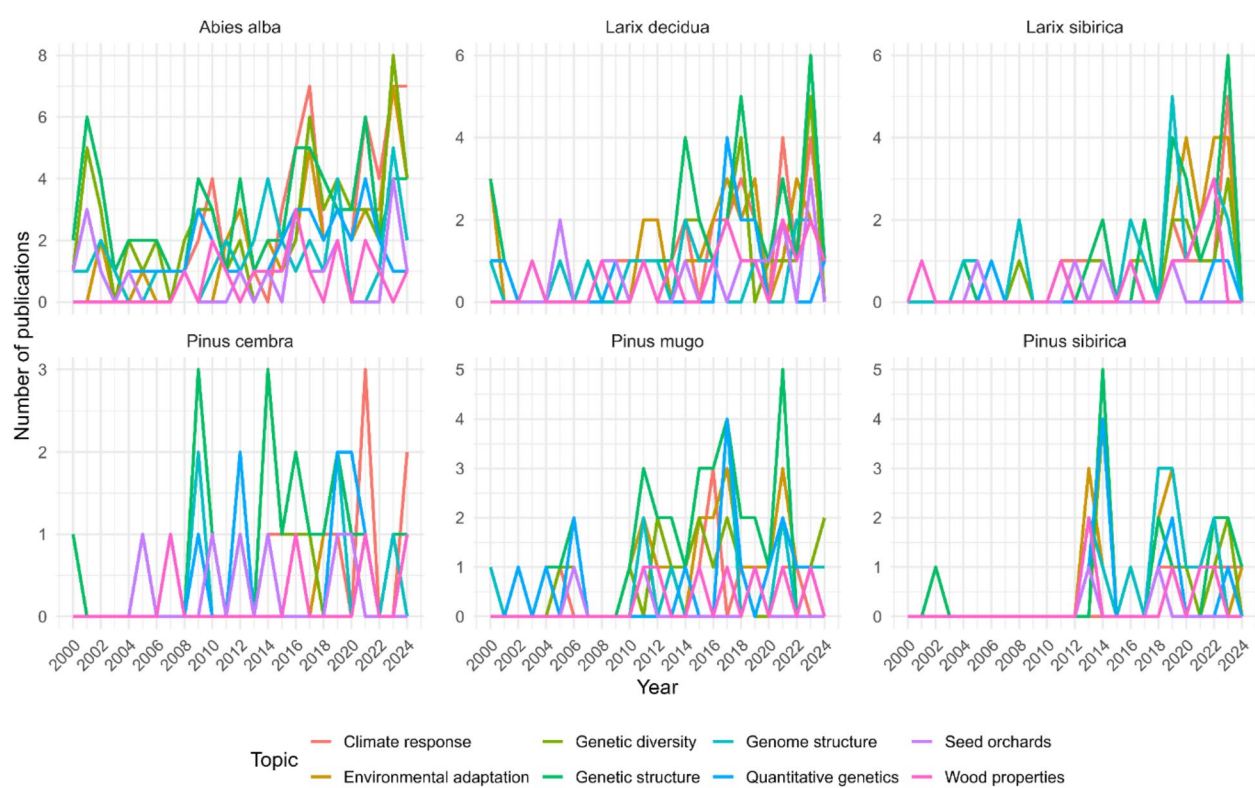


Fig. 9 Topic occurrence trends of the six other conifer species examined, excluding *Picea abies*, for eight predefined research topics in alpine forest genomics over the 2000–2024 period. Each panel represents one of the six tree species in focus, showing the annual number of publications in which the species is associated with each topic. Colors correspond to thematic categories

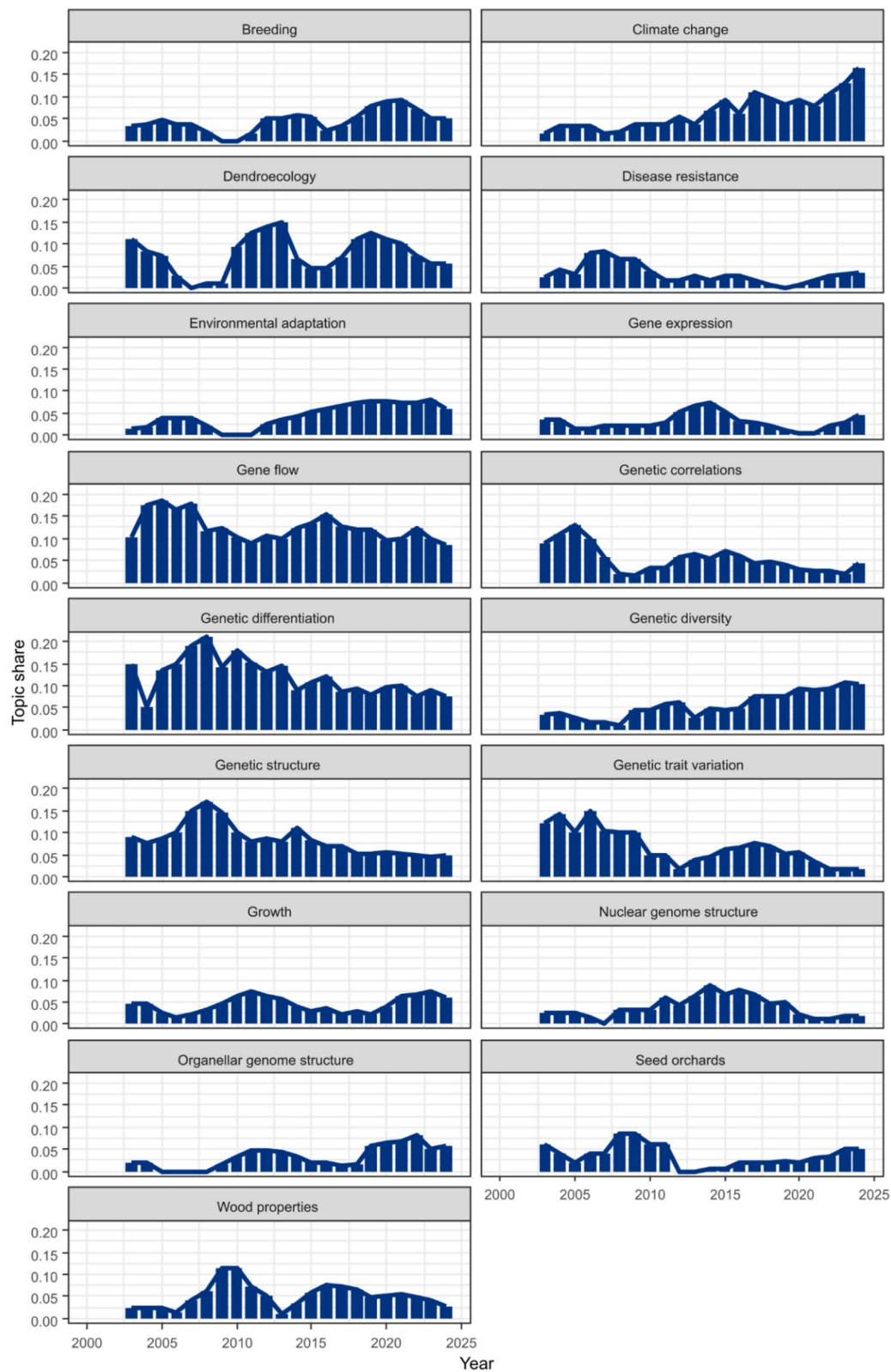


Fig. 10 Publication share smoothed over intervals of 4 years for each of 17 research topics from 2000 to 2024 identified in the 662 publications

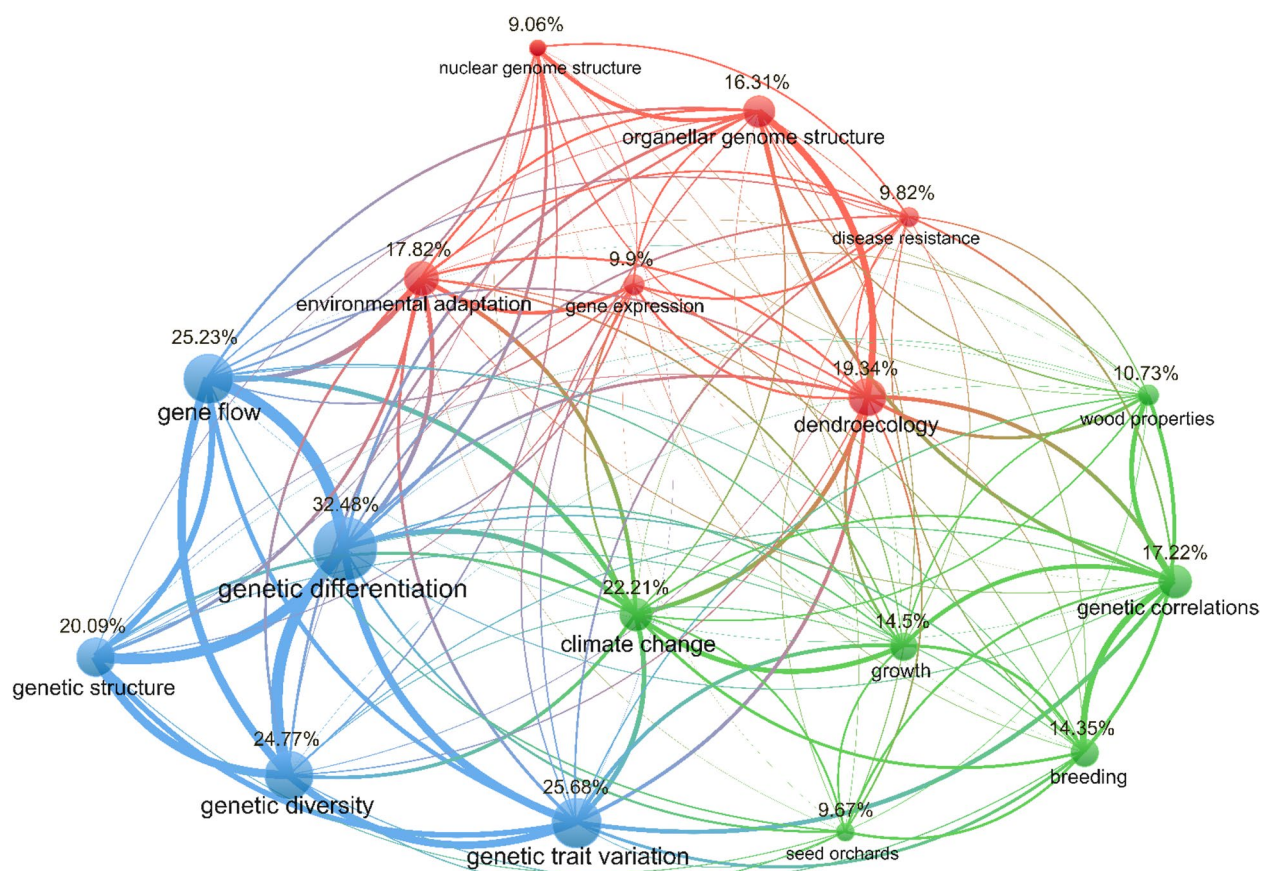


Fig. 11 Co-occurrence network of all 17 predefined research topics in alpine forest genomics over the 25-year period (2000–2024). The spatial proximity of items reflects the relative strength of association and thematic similarity between topics. Topics within the same cluster are indicated by matching colors (red: adaptive and quantitative genomics; blue: population structure and genetic diversity; green: functional and trait genomics). Font size and node size correspond to the number of publications in which each topic appears, while connecting lines represent co-occurrence relationships; the thickness of each line denotes the frequency with which two topics co-occur in the same publication. The percentage shown above each node illustrates that topic's proportion of occurrence across all publications

Studied species	Published nuclear reference genome assembly [version; (NCBI) accession number or link; reference]	Not (yet) published reference genome assembly [reference]	Transcriptome assembly [reference]	Plastid genome assembly [reference]	Mitochondrial genome assembly [reference]
<i>Abies alba</i>	Abal.1_1; https://treegenesdb.org/FTP/Genomes/Abal/ ; Mosca et al. (2019)		Roschanski et al. (2013)	Li et al. (2019)	Kersten et al. (2022)
<i>Larix decidua</i>				Wu et al. (2011)	
<i>Larix sibirica</i>	LarixSibirica0.16; GCA_004151065.36; Kuzmin et al. (2019), Bondar et al. (2022)			Bondar et al. (2019)	NCBI GenBank MT797187-MT797195; Putintseva et al. (2020)
<i>Picea abies</i>	Pabies01; GCA_900067695.1; Nystedt et al. (2013)	chromosome level assembly: Nilsson et al. (2025)	Heer et al. (2016); Nilsson et al. (2025)	Nystedt et al. (2013)	Sullivan et al. (2020)
<i>Pinus cembra</i>			Rellstab et al. (2019); Köbölkuti et al. (2020)	NA	

Studied species	Published nuclear reference genome assembly [version; (NCBI) accession number or link; reference]	Not (yet) published reference genome assembly [reference]	Transcriptome assembly [reference]	Plastid genome assembly [reference]	Mitochondrial genome assembly [reference]
<i>Pinus mugo</i>				Sokołowska et al. (2021)	
<i>Pinus sibirica</i>				Baturina et al. (2019)	

Table 4 Overview of available genomic resources of related conifer species

Related species	Published nuclear reference genome assembly [version; (NCBI) accession number or link; reference]	Not (yet) published reference genome assembly [reference]
<i>Larix kaempferii</i>	LKA_r1.0; GCA_027924585.1; Shirasawa et al. (2024)	
<i>Larix kaempferii</i>	version 1.0; GWH PRJNA58704-1, https://ngdc.cncb.ac.cn/gwh/Assembly/24470/show ; Sun et al. (2022)	
<i>Pinus albicaulis</i>	WBP_1.0; GCA_034641835.3; Neale et al. (2024)	
<i>Pinus lambertiana</i>	Pila.1_5; https://treegenesdb.org/org/Pinus-lambertiana ; Stevens et al. (2016)	
<i>Picea mariana</i>	Pmariana_40-10-1_v1; GCA_032191745.1; Lo et al. (2023)	
<i>Pinus massoniana</i>	NA; PRJNA1240911; Nilsson et al. (2025)	
<i>Pinus sylvestris</i>		chromosome level assembly: Nilsson et al. (2025)
<i>Pinus tabulaeformis</i>	CPIR1; GCA_031772625.1; Niu et al. (2022)	
<i>Pinus taeda</i>	Ptaeda2.0; GCA_000404065.3; Zimin et al. (2014); Neale et al. (2014)	

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Authors' contributions

K.B.B. and Z.A.K. contributed equally to this study. C.R., K.B.B., Z.A.K., M.W., and N.A.M. conceptualized the study; C.R. carried out the literature search; C.R., K.B.B., Z.A.K., M.W., and N.A.M. designed the survey; Z.A.K., T.H., K.B.B., C.R., and N.A.M. analyzed data; all co-authors wrote and revised the manuscript.

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Data availability

All data supporting the findings, i.e. the references used in the bibliometric analyses, as well as the survey answers and corresponding categories, are available in the Zenodo repository: <https://doi.org/10.5281/zenodo.22644199>.

Declarations

Ethics approval and consent to participate

This study involved a voluntary, professional survey of scientists within AForGeN. Because the research did not involve patients, medical data, or vulnerable populations, formal ethics committee approval was not required. However, the survey and overall research were conducted in strict accordance with the guidelines for "Good Scientific Practice" of the German Research Foundation (DFG), as implemented by the Northwest German Forest Research Institute.

Informed consent was obtained from all individual participants (AForGeN members) who completed the survey included in this study.

Competing interests

The authors declare no competing interests.

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