Forest biodiversity and ecosystem services from spruce-birch mixtures: The potential importance of tree spatial arrangement

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ARTICLE INFO

ABSTRACT

There is increasing empirical support for the biodiversity and ecosystem service (ES) benefits of mixed-species production forests. However, few studies control for the spatial arrangement of the trees within mixtures to determine the influence that clustering the tree species (patch scale mixtures), versus evenly dispersing them (intimate scale mixtures), may have for biodiversity and ES outcomes. To highlight the potential implications of altering tree spatial arrangement in mixtures, and the need to fill related knowledge gaps, here we provide a qualitative multi-disciplinary overview of ecological and socio-economic drivers with the potential to alter biodiversity, ecosystem services, and management-related outcomes from patch versus intimate scale mixtures. We focused our overview on even-aged mixtures of Norway spruce (*Picea abies*) and birch (*Betula pendula* or *B. pubescens*) in Sweden, which enabled us to contrast findings within a biogeographical and silvicultural setting. Specifically, we targeted implications for biodiversity (understory vascular plants, epiphytic lichens, saproxylic beetles, birds), biomass production, harvesting costs, management ease, recreation and aesthetics, cervid game, as well as abiotic and biotic risks (wind, fire, pathogens, pests, browsing damage). In the absence of direct empirical evidence, we primarily relied on expert inference from theory and relevant empirical studies sourced from the Fennoscandian region, and further afield if needed. Collectively these efforts allowed us to develop a number of informed hypotheses indicating that for spruce-birch mixtures in this region, patch scale mixtures may have the potential to favour the diversity of several forest dependant taxonomic groups, cervid game and reduce harvesting costs, whereas intimate mixtures may have the potential to reduce pathogen and pest damage, and likewise, potentially benefit production outcomes. Current knowledge was too limited, inconsistent or context dependant to even tentatively infer outcomes for fire risk, wind damage, browsing damage, management ease, recreational and aesthetic outcomes. We emphasize that our hypotheses require testing, but are sufficient to (1) highlight the likely importance of spatial-scale to biodiversity and ecosystem services outcomes in mixed-species production forests, (2) caution against generalization from mixture studies that lack scale considerations, and (3) motivate the targeted consideration of spatial grain in future mixture studies.

1. Introduction

One third of the world´s forest area is used primarily for the production of wood biomass (FAO, 2020), and a decreasing proportion of the world´s natural forests are left standing, unfragmented, or unaltered (Curtis et al., 2018; Haddad et al., 2015). The choices made when managing the world's extensive production forests therefore have important and wide ranging implications, affecting everything from biodiversity and the provision of biomass for building and energy, to carbon sequestration and the availability of environments for recreation (Felton et al., 2020b; Ranius et al., 2018; Roberge et al., 2016b). The net result of these decisions is increasing reliance on intensively man-

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Monoculture

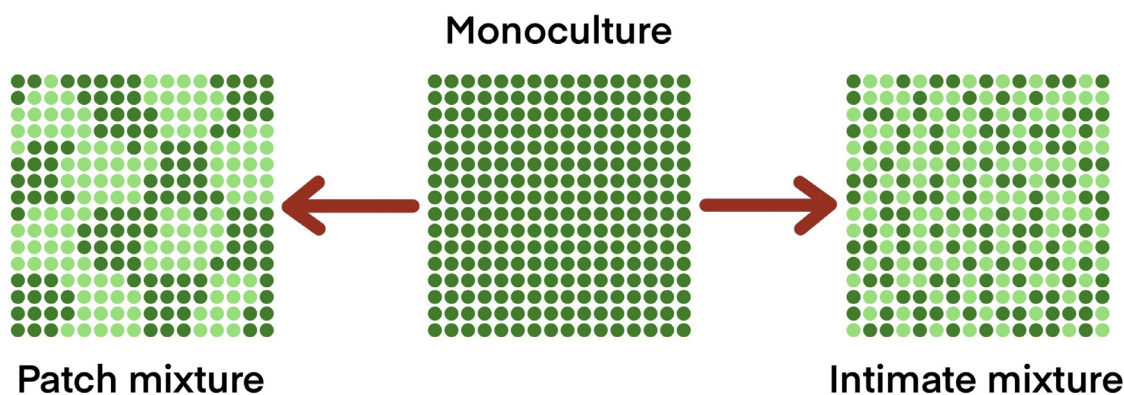## Patch mixture   ## Intimate mixture

Fig. 1. An illustration using dark and light green dots to indicate different tree species, as found within a stand monoculture (centre square), and two mixture alternatives which differ in the spatial-scale at which the tree species are mixed within the stands (left and rightmost squares) at harvest time. In both mixture alternatives, each tree species provides 50% of the stand basal area. The leftmost stand is representative of a patch mixture whereby conspecifics are grouped to create replicated clusters of each tree species. The rightmost stand is representative of an intimate mixture whereby the different tree species are approximately evenly dispersed through the stand in similar proximity to conspecifics as to the other species.

aged production stands to meet global requirements for timber, wood fibre and bioenergy (Payn et al., 2015; Warman, 2014). In many cases, these stands are managed as even-aged monocultures (Liu et al., 2018; Puettmann et al., 2015), in part because of the ease provided by single tree species management, as well as the large amounts of biomass per unit area that intensive production forestry can provide (Van der Plas et al., 2016). Unfortunately, these structurally simplified stands often fail to provide suitable habitat for many forest species (Lindenmayer and Franklin, 2002), as well as the variety of ecosystem services (ES) that societies increasingly demand (Lindahl et al., 2017; Messier et al., 2021; Schwenk et al., 2012).

Mixed tree species approaches to forestry (hereafter mixtures) involve stands designed around the production of two or more tree species, and appear to be less prone than monocultures to stark trade-offs between production and other ES (Van der Plas et al., 2016). Importantly, the increased tree diversity and higher structural complexity of mixtures is often associated with improved habitat conditions for many species (Ampoorter et al., 2020; Cavard et al., 2011; Felton et al., 2010), and there is growing evidence that within some contexts, mixtures can provide better production and economic outcomes than monocultures (Bielak et al., 2014; Huang et al., 2018; Jonsson et al., 2019; Pretzsch et al., 2017). Furthermore, the risks, uncertainties and increasingly observed damage inflicted on forests by climate change (Allen et al., 2010; Seidl et al., 2014b), can favour the use of mixtures to either mitigate specific risks (Morin et al., 2014), or give managers the adaptive capacity to pursue alternative directions of stand development (Pawson et al., 2013; Seidl et al., 2018). Mixtures are also being advocated due to the more favourable environments provided for recreation and non-wood forest products (Felton et al., 2016b; Gamfeldt et al., 2013).

Whereas the evidence continues to accumulate, and often favours mixtures over monocultures (Felton et al., 2016b; Huuskonen et al., 2021), substantial uncertainties remain (Coll et al., 2018). A key uncertainty is whether spatially clustering the tree species (patch scale mixtures) within a stand, or evenly dispersing them (intimate scale mixtures), has important implications for biodiversity and ES outcomes. Just as there is no objective demarcation as to when a monoculture becomes a mixture (Bravo-Oviedo et al., 2014), so too is there no objective demarcation between intimate and clustered mixtures. However, the existence of a continuum between two identified positions does not make these positions indistinguishable, and there is reason to expect that mixture outcomes may vary at sufficiently distinguished positions

along this spatial scale continuum (see Fig. 1). For example, some studies suggest that altering the proximity and proportion of distinctive tree species has the potential to influence the stand's overall resilience to natural hazards (Griess et al., 2012). Similarly, the complexity of forestry operations will likely differ depending on whether managers are faced with discernible patches of single tree species, rather than intimately mixed tree species (Felton et al., 2016b). Furthermore, the placement and proximity of different tree species with distinct physiognomies and ecologies, could be expected to alter environmental conditions for biodiversity (Hedwall et al., 2019), as well as the exposure of individual trees to forest pests and pathogens (Jactel et al., 2009). Although such arguments can be made as to why the spatial grain of mixtures could matter to biodiversity and ecosystem services outcomes, more targeted insights are needed regarding the specific trade-offs or synergies that may arise in particular mixture outcomes. Expert insights are especially valuable in this regard as few experiments have addressed this topic, especially with respect to specific tree-species mixture alternatives, and in regards to the combined breadth of potential biodiversity and ecosystem services outcomes of relevance to forest owners, managers and policy makers.

Here we highlight the potential implications of altering tree spatial arrangement in mixtures, and the need to fill related knowledge gaps, by providing a qualitative multi-disciplinary overview of ecological and socio-economic drivers with the potential to alter biodiversity, ecosystem services, and management-related outcomes from patch versus intimate scale mixtures. To do so we focused our overview on even-aged Norway spruce (*Picea abies*) and birch (*Betula pendula* or *B. pubescens*) mixtures in Sweden, which enabled us to contrast outcomes within a biogeographical and silvicultural setting. We focused on this tree species mixture because i) it is one of the most prevalent and well-studied conifer and broadleaf tree species alternatives in Fennoscandia, and ii) it involves tree species with distinctive taxonomic and ecological traits (a shade tolerant late-successional conifer vs. an early-successional light demanding broadleaved species) that we expected to better distinguish mixture-scale implications. We evaluated the potential implications of altering the mixture-scale for biodiversity, and a range of ecosystem services (MEA, 2005), including provisioning, cultural and regulatory services. We also evaluated management ease and harvesting costs because of their relevance to provisioning goals. To address this issue in the widespread absence of direct empirical testing, we primarily relied on expert inference from theory and relevant empirical studies sourced from the Fennoscandian region and further afield if needed. Because we relied on expert perspectives in an under-researched area at the frontier

of current knowledge, we consider our results to be informed hypotheses to be tested, rather than as empirically-justified conclusions. Our primary aim was to highlight the importance of bridging this knowledge gap regarding mixtures, and how not considering the spatial-scale of the mix may lead to inconsistent outcomes and thus unreliable generalizations regarding the biodiversity and ES contributions of mixtures. Although we focus on a single mixture alternative within a targeted biogeographical context, we see our work as directly relevant to growing international awareness of the potential biodiversity and ecosystem service benefits from diversifying silviculture to include a wider variety of less intensive practices (Puettmann et al., 2015), that better match natural forest disturbance regimes and tree species compositions (Ampoorter et al., 2020; Felton et al., 2020a).

2. Background

2.1. Sweden's forest context

Forests cover 70% of Sweden's land area, and comprise both temperate and boreal biomes, and most of the productive forest area is managed using intensive even-aged conifer-dominated approaches for the production of timber, pulp and bioenergy. Norway spruce is the most common tree species by volume on productive forest lands in Sweden (40% of standing volume) (SFA, 2014). There are increasing concerns regarding biodiversity loss from the extensive use of intensive conifer forestry (Felton et al., 2020a; Lindbladh et al., 2014), decreased forest resilience and susceptibility to disturbance (Lidskog and Sjödin, 2014; Valinger and Fridman, 2011), and decreased opportunities to increase the provision of non-wood forest products (Felton et al., 2016a; Lindahl et al., 2017). It is within this context that Swedish governmental agencies actively support increased use of mixed-broadleaf production forests (Bergquist et al., 2016; SOU, 2013).

2.2. Spruce-birch mixtures in Sweden

In Sweden, Norway spruce is primarily managed as even-aged stands, with the majority felled using clearcutting with retention (Felton et al., 2020a) after 60–100 year rotations (depending on site productivity and interest rates; Felton et al., 2017; Roberge et al., 2016a), and then regenerated by scarification and planting (Holmström et al., 2021; SFA, 2021). The most prevalent size of clearcuts in Sweden is between 4 and 10 ha (SFA, 2021), and scarification of these areas often unintentionally facilitates the natural regeneration of birch (Holmström et al., 2017), which can occur in high densities (Holmström et al., 2019). At an early stage in stand development, pre-commercial thinning is used to determine the species composition, proportion, and stem density of the stand (Fahlvik et al., 2015a; Holmström et al., 2016), with height relations between the tree species an important additional determinant of whether the stand will be managed as a mixture throughout the rotation (Fahlvik et al., 2015a; Holmström et al., 2015). It is also during this early stage in the rotation that owners can decide to favour patch versus intimate scale mixtures via targeted thinnings.

2.3. Defining intimate and patch-scale mixtures

For our study purposes, mixtures are stands designed around the simultaneous (even-aged) production of two or more tree species, none of which comprises ≥ 70% of stand basal area at final harvest (Fig. 1). There is no objective threshold delineation between an intimate versus a patch-scale mixture, and under natural conditions, the degree of dispersal or clustering of trees will vary throughout the stand. Accepting this subjectivity, for our purposes we define intimate mixtures as stands in which the tree species are evenly dispersed through the stand in similar proximity to conspecifics as to hetero-specifics at the time of harvest. We define patch-scale mixtures as stands in which tree conspecifics are grouped to create replicated clusters of each tree species

within the stand, to form patches of approximately 100–400 m^2 in size at the time of harvest. This choice of patch size is a compromise between clustering tree species sufficiently to distinguish outcomes from intimate scale mixtures (not too small), while avoiding patch sizes so large as to overlap with small monocultures (not too large). Furthermore, although differences in height growth dynamics will result in varying tree sizes during stand development, we deemed two-storied stand characteristics at the time of final harvest as being outside the scope of this paper (Kelty, 2006).

2.4. Expert contributions

Participating researchers were asked to provide an evidence-based overview of whether or not ecological and socio-economic drivers exist, that could favour the use of patch versus intimate mixtures in terms of specific biodiversity and ecosystem services outcomes of a mixture. The research topics assessed included biodiversity (understory vegetation, birds, saproxylic beetles, lichens), as well as major categories of ecosystem services (MEA, 2005), including provisioning services (wood biomass production), cultural services (recreation and aesthetics, cervid game (deer family Cervidae)), and regulatory services (reduced risks of pests, pathogens, fire, wind throw, and browsing damage). We placed cervid game within cultural services due to the strong cultural aspect of hunting in Sweden, while acknowledging that cervids also provide non-wood provisioning services, as well as being an important component of, and influence on, forest biodiversity. We also summarized additional forest management considerations which are likely to be of importance to decision makers, but which do not readily fit within the other ES categories considered. These included management ease and harvesting costs, which for convenience, we place with provisioning services. The topics assessed were targeted towards issues frequently raised by forest stakeholders (e.g. production outcomes, damage risk, recreation, biodiversity) when deciding amongst production forest alternatives (Lidskog and Sjödin, 2014; Lodin et al., 2017), while also being filtered by the expertise of participating researchers, and thus to some extent subjective. To capture relevant literature, electronic databases (Web of Science, Scopus, google scholar), were searched using different combinations of Boolean search terms. A core set of search terms, "Picea abies" or "Norway spruce" and "Betula" or "birch*", as well as variants of "mix*", "polyculture*", "admix*", "multi-species*", "multiple species", "patch*", "intimate*", "scale*", "grain*", "individual*", "dispers*", "intermix*", "group*", "cluster*", "neighbo*", "tree* level*" or "stem* wise*" were used by participants, and supplemented with additional search terms targeted to capture specific topics (e.g. "pest*", "pathogen*", "bird*", etc.). Search terms were run in separate or limited combinations depending on the requirements of the database used. We also obtained results from books, government reports, and the reference lists of published studies. Due to the range of issues we address, our results provide a condensed overview, rather than as a basis for considering the entirety of potential costs and benefits derived from each mixture type.

3. Results

3.1. Biodiversity

3.1.1. Understory vascular plants

The tree species composition and canopy structure of the overstory are important drivers of the diversity and composition of understory vegetation, due to the regulation of factors including temperature, light, water, and soil nutrients. Whether the scale of tree species mixing has an effect on understory plants, depends on; (1) if there are plant species that explicitly depend on the conditions that intimately mixed tree species canopies create (Barbier et al., 2008; Cavard et al., 2011), (2) the scale (distance of the effect) at which the tree canopy influences the composition of understory plants, and (3) the influence of covariates, such as

stand density, on these factors (Hedwall et al., 2019). To our knowledge, no single study tackles all of these aspects, and importantly, few studies evaluate the full gradient of tree species mixing from a monoculture of one species, to a monoculture of another (see refs in; Barbier et al., 2008; Cavard et al., 2011). In addition, very few understory plant species seem to be exclusively connected to intimate mixtures. However, a study spanning the gradient from Norway spruce (*Picea abies*) to pure birch (*Betula* spp.) monocultures, found approximately 10% of understory plant species (vascular and bryophytes) had their highest probability of occurrence in mixtures, but most of these species were also prevalent in either monoculture (Hedwall et al., 2019). In terms of the distance at which tree species effect understory plant communities, a study by Saetre (1999) of understory vegetation in an 18 m high spruce-birch mixture, found that single trees of both species influenced the vegetation ~5 m from their trunks, while Hedwall et al. (2019) determined that the effect of the tree layer on understory vegetation generally has very little impact beyond 8–9 m. Importantly, the scale at which single trees influence the understory vegetation will most likely depend on both the crown size and tree height.

Hedwall et al. (2019) also found that at a basal area above 30 m^2 ha^{-1}, the cover of understory vascular plants remained below 10% regardless of whether the proportion of birch was 30% or 0%. As there is less shading effect of neighbouring spruce in patches, we therefore suggest, at least for high spruce stand density, that clustering birch into patches rather than intimately may provide greater insolation of the understory in spruce dominated stands (ibid.), and thereby greater overall habitat variation and niche space in the stand understory. Patch scale mixtures may thus be favoured over intimate mixtures if the goal is to enhance vascular plant diversity. Importantly, the associated increase in vascular plants due to the larger share of broadleaves, and concomitant changes to insolation, leaf litter, and competition from vascular plants, may result in a decline in understory bryophyte species richness and abundance (Cavard et al., 2011).

3.1.2. Epiphytic lichens

Epiphytic lichen communities depend to a large extent on the environmental conditions provided by their host tree species, which dictate everything from bark structure and acidity, as well as the understory humidity and insolation as influenced by the tree species' total leaf area (Ellis, 2012). Due to differences in the leaf area of birch versus spruce trees, as well as their being deciduous rather than evergreen (Barbier et al., 2008; Cavard et al., 2011), birch trees, and to a larger extent patches of birch, allow higher understory light levels than Norway spruce grown at similar densities (Hedwall et al., 2019). Though no studies empirically contrast the lichen communities of spruce-birch mixtures at varying mixture scales, patches of Norway spruce can be expected to favour distinct lichen species assemblages specialized on stable conditions of lower light and humidity, in contrast to those assemblages favoured by patches of birch (Felton et al., 2010; Marmor et al., 2012). Note however, that if canopy cover is very dense, light levels may be so low as to prevent even low-light adapted species from establishing (Hilmo et al., 2009; Nirhamo et al., 2021). The varying spatial juxtaposition and distances found amongst patches of Norway spruce and birch within a stand, and the associated higher variance in light and humidity amongst such patches, should also benefit a broader range of lichen species requiring specific combinations of environmental conditions that are likely to result; such as macrolichens favoured by both higher light levels (Uliczka and Angelstam, 1999). For this reason, we preliminarily suggest that patch level mixtures may provide increased habitat and niche space relative to intimate mixtures, and thus support more diverse epiphytic lichen communities; though resultant diversity will be greatly curtailed by production forest rotation lengths (Dettki and Esseen, 2003).

3.1.3. Saproxylic insects

Saproxylic insects use dead and decaying wood as habitat, often at a particular stage of decay. This results in a limited time-window within which a habitat may be colonised. Because of the ephemeral nature of their habitat, saproxylic species often have good dispersal abilities (Jonsell, 2007; Komonen and Müller, 2018), and the spatial scale at which mixtures are created is unlikely to have an effect *per se* on the probability of colonisation. Likely for this reason, no studies were found which tested the response of saproxylic species at this spatial grain. Studies done over larger spatial scales, and not involving old growth, have found that the properties of the wood itself are much more important than properties of the stand or surrounding landscapes (Ranius et al., 2015; Sverdrup-Thygeson et al., 2014). Thus, the main influence that spatial grain of the mixture may have on habitat suitability for saproxylic insects, is expected to occur through the properties of the dead wood (e.g. insolation).

Sun exposure is an important factor for saproxylic insect species, and many are primarily associated with sun-exposed environments (Kouki et al., 2001; Lindhe et al., 2005). In particular, high stem densities in intensive production forests can be problematic, as even if dead wood is suitable in other ways, being too shaded and cold may render it unsuitable as habitat (Lindhe et al., 2010). For a given stand density, a patch of birch will allow a higher level of understory insolation than is provided by an otherwise equivalent patch of Norway spruce trees (Hedwall et al., 2019). Compared to patches, intimate mixtures run the risk of more uniform and lower levels of understory insolation, because more of the birches are then shaded by spruce (see section 'understory vascular plants'). This effect is correlated with stronger overgrowth by mosses, which further limits habitat suitability for many saproxylic insects (Dynesius et al., 2010). In contrast, patch scale mixtures may allow for more sun exposed micro-sites to develop, and we therefore tentatively suggest that patch scale mixtures may be more favourable for the diversity of saproxylic insect species.

3.1.4. Birds

Forest bird species vary in sensitivity to differences in tree species composition and forest structure at various spatial scales with corresponding net implications bird diversity (Jokimäki and Huhta, 1996; Lemaitre et al., 2012). In this regard, Peck (1989) found that a small number of an additional tree species within stands had a seemingly disproportionate positive effect on the bird diversity; a finding replicated by several studies in Sweden which have detected positive impacts on bird diversity of broadleaf trees found at basal area concentrations of less than 20% in Norway spruce dominated stands (Felton et al., 2011; Lindbladh et al., 2017). Unfortunately, the published evidence is relatively limited and somewhat contradictory with respect to which spatial grain of mixture creation best enhances bird diversity.

Two studies in England advocate the use of intimate mixtures in otherwise conifer dominated forests, justified by the inferred benefit of dispersing and thereby maximising the positive contribution of broadleaf trees to bird communities (Bibby et al., 1989; Donald et al., 1998). However, a study in Scotland suggests instead that concentrating broadleaves into patches will yield greater biodiversity benefits for bird communities (French et al., 1986), due to the need to meet the territory requirements of broadleaf specialists. French et al. (1986) suggests that patch sizes of 50–100 m in diameter (larger than those considered here), or clusters of smaller patches, should allow territory establishment by birds associated with a particular tree species. Furthermore, patches of birch may favour increased shrub cover in the understory (Hedwall et al., 2019), which is often an important driver of forest bird diversity (Cavard et al., 2011; Donald et al., 1998). A recent Swedish study conducted in stands spanning the spectrum of Norway spruce dominated, spruce-birch mixtures, and birch dominated stands, found that forest bird diversity is highest in stands dominated by birch, and also emphasizes the importance of canopy openness and a well-developed understory vegetation layer for bird diversity (Felton et al., 2021). We therefore suggest that

the collective evidence available tentatively favours the use of patch-scale mixtures to enhance bird diversity.

3.2. Provisioning services and related considerations

3.2.1. Wood biomass production

We found only a single study comparing production outcomes between patch versus intimate scale mixtures of Norway spruce and birch mixtures. This modelling study, which also included pine, found no significant differences in above-ground wood volume production (Fahlvik et al., 2015b). More generally, Mielikäinen (1985) found higher volume production in intimate scale mixed spruce – birch stands compared to pure spruce stands, whereas some other studies indicate that volume production in spruce-birch mixtures decreases with birch prevalence (Fahlvik et al., 2015b; Frivold and Frank, 2002). Studies of "over-yielding" and associated theoretical expectations may also provide relevant insights. Over-yielding is defined as greater productivity than the mean (weighted by species proportion) of component species productivities in their respective monospecific stands (Pretzsch et al., 2017). Although the most productive tree species in a mixture tend to determine total production levels, there are many examples of over-yielding, including several supportive studies involving birch-spruce mixtures (Huuskonen et al., 2021). For example, in central Europe overyielding levels of 11–30% are reported in mixtures, with the overyielding response tending to increase when using tree species differing in shade-tolerance (Pretzsch and Zenner, 2017). Therefore, whereas few studies were found indicating overyielding in Norway spruce and birch mixtures (Shanin et al., 2014), and some studies highlight the importance of higher site fertility and the use of *B. pendula* specifically to enhance mixture production outcomes (Felton et al., 2016b; Huuskonen et al., 2021), the respective status of spruce and birch as shade tolerant and light demanding tree species indicates the potential for overyielding if intimately mixed (Huuskonen et al., 2021; Pretzsch et al., 2017). One important caveat is that overyielding mainly appears in denser stands without recent management interventions (Brunner and Forrester, 2020; Huuskonen et al., 2021).

In conclusion, we find insufficient empirical data to confidently determine whether intimate or patch scale mixtures achieve better production outcomes. However, the results of over-yielding studies and associated theoretical expectations appear to indicate that intimate mixtures may be more favourable than patch mixtures in terms of above-ground biomass production, though this hypothesis requires field experimentation and validation.

3.2.2. Harvesting costs and management ease

We found no studies comparing intimate and patch mixtures in terms of logging costs or costs for silvicultural operations. Nevertheless, useful insights can be gained by considering why mixtures are costlier than monocultures to harvest, which primarily results from the added costs of management and timber assortments that need to be handled separately (Nichols et al., 2006). One estimate is that harvesting mixtures is 3% more expensive during thinning, and 1–2% more expensive during final felling than monocultures (Sirén and Aaltio, 2003). If patch mixtures allow each tree species to be managed distinctly with respect to silvicultural regimes (e.g. thinning), then patch-scale mixtures may reduce logging costs relative to intimate mixtures. However, managing trees in this regard may not be economically feasible, due to increased costs of logging operations in patch patterned stands, as well as the added costs of moving harvesting machinery between logging sites at different times. This highlights the complexity of addressing issues concerning management ease, as a management option (e.g. patch scale mixtures) may decrease the complexity of silvicultural treatments, while increasing logistical complexity. A key additional consideration is whether the birch component of these mixtures is created with improved material, or naturally regenerated birch. If natural regeneration is used, it may be more difficult to create and maintain an intimate mixture, due to

the higher growth capacity of improved spruce seedlings (Jansson et al., 2017). For naturally regenerated birch, patch mixtures may be the more viable option.

In summary, relative to intimate mixtures, patch mixtures may reduce harvesting costs associated with assortments, and also increase the potential for combining genetically improved Norway spruce with slower growing naturally regenerated birch. Whether management ease improves with patch mixtures remains unclear.

3.3. Cultural services

3.3.1. Aesthetics and recreation

We found four relevant articles directly assessing people's preference for conifers, broadleaves, and mixtures in relation to forest aesthetic and recreational experiences. Of these studies only one contrasts Norway spruce and birch (Gundersen and Frivold, 2008), and no studies directly contrasted patch versus intimate scale mixtures. Nevertheless, from these studies a complex but relevant picture emerges. Importantly, the term mixture in these studies appears to more readily align with what we define as an intimate mixture. When people consider the recreational value of forests, they often express preferences for the within-stand variation in environments that is provided by mixtures over monocultures (Abildtrup et al., 2013; De Meo et al., 2015; Filyushkina et al., 2017). However, some studies also find a preference for the variation in conditions that is provided between differing stand types, which may or may not override the importance of within-stand variation (Filyushkina et al., 2017). Notably, people can also express a preference for pure birch stands over pure conifer stands, with additional preferences expressed for openness, visibility, light and stratification (Gundersen and Frivold, 2008).

In summary, there is insufficient evidence to conclude which spatial grain (patch or intimate scale) people generally prefer if given the choice. Nevertheless, many forest users suggest that forest variation, openness, and light are influential. What remains unclear is in which direction this influences the preferences of forest users. If patch scale mixtures more readily reach preferred levels of understory openness and light, and such patches of birch are not so large to counter people's preferences for variability, then perhaps patch-scale could be favoured. This remains speculative until further studies are conducted.

3.3.2. Cervid game

Large herbivores of the family Cervidae are an important cultural and hunting resource in Sweden, for which the annual gross value of recreational benefits and food provided from game meat was estimated to be over 300 million USD in 2012 (Boman and Mattsson, 2012). These herbivores therefore provide people both with cultural (recreational, hunting) and provisioning ES (game meat production). Moose (*Alces alces*) and roe deer (*Capreolus capreolus*) are the most abundant and widely distributed forest cervids in the region. Especially with respect to moose, birch is often a staple food eaten in proportion to its availability, whereas for both species, young Norway spruce is normally only eaten in minor quantities (Månsson et al., 2007; Mattila and Kjellander, 2017; Wam and Hjeljord, 2010). Importantly, understory plants are vital to cervid diets, including amongst red deer (*Cervus elaphus*) and fallow deer (*Dama dama*) which also occur in the region, and can comprise more than half of summer foods consumed (Wam and Hjeljord, 2010). Assuming increased understory insolation (see "Understory vascular plants"), birch patches are likely to provide more biomass of understory vascular plant food resources, for a higher proportion of the rotation period, than if intimately mixed with Norway spruce. Birch patches could likewise increase understory plant diversity within a stand (Hedwall et al., 2019), and thereby provide more varied nutritional quality to choose from, with resultant benefits for cervid body mass (e.g. moose, Felton et al., 2020c). Finally, patch versus intimate mixtures may influence the cervids' use of a stand due to risk perception. Large cervids like the moose can seek mature spruce patches for shelter from

humans, other predators, heat or inclement weather (Allen et al., 2014; Bjørneraas et al., 2012), while smaller cervids can seek birch patches for their concealing understory vegetation (Borkowski and Ukalska, 2008; Bowyer et al., 1998).

For these reasons, we suggest that patch scale mixtures of spruce and birch are more likely to benefit cervid game than intimate mixtures, primarily due to associated increases in understory biomass and -diversity, as well as more diverse sheltering cover for more of the rotation period. However, and most importantly, due to the large home ranges of these animals, a positive effect on reproduction and survival would require landscape or regional scale application.

3.4. Regulatory services

3.4.1. Wind

Wind damage depends on the force of the wind, and the trees' resistance, as determined by the tree's mechanical properties including height, diameter, root anchorage, whether in leaf or not, etc. (Gardiner et al., 2016). With respect to Norway spruce and birch mixtures, spruce is generally more susceptible to wind damage than birch (Mason and Valinger, 2013), and spatial arrangements within a stand can reduce as well as increase the probability of wind damage due in-part to micro-sheltering effects (Bauhus et al., 2017). For example, interactions between swaying crowns can increase stability (Moore and Maguire, 2004), but evidence suggests that interspecific interlocking and grafting of root systems is extremely rare (e.g. Eis, 1972). Hence, increased stability because of root contacts effect appear less likely in interspecific than in conspecific forest stands (Bauhus et al., 2017). Furthermore, the spatial grain of the mixture can affect stand heterogeneity, with complex implications for the probability of wind damage (Kamimura et al., 2019; Seidl et al., 2014a). For example, in widely spaced low density stands, individual trees can also become more stable because they develop a low height-to diameter ratio and a large root system (e.g. Cremer et al., 1982). However, because of deeper wind penetration, the forces acting on individual trees in open stands can be much higher than in dense stands (Ruel, 1995).

Several empirical European studies indicate that mixing broadleaves with conifers, reduces the susceptibility of mixed forests to wind damage (see Jactel et al., 2017). Of particular interest is whether the susceptibility to damage in mixed stands is reduced only in proportion to the share of the more stable tree species, or if the stability of the more susceptible species is itself increased by the mixture (Dhôte, 2005; Griess and Knoke, 2011). If the susceptible species benefits, then this effect is expected to occur in the contact zones between the tree species, and thus the resultant effect size would be higher in intimate than in patch-scale mixtures (Griess and Knoke, 2011). A post-storm demographic analysis in southern Sweden found that the probability of wind damage to Norway spruce was 2.5–3.5 times higher if surrounded by conspecifics (20 m radius), than if mixed with 30% birch (Valinger and Fridman, 2011). It is unclear however whether the reduced damage in stands with more birch is only in proportion to the share of more stable species, or because of a mixture effect, or due to other confounding factors such as stand density, site conditions, silvicultural practices, etc. (see Bauhus et al., 2017). In a German study, Griess et al. (2012) found that the probability of spruce survival (from wind and insects) increased if broadleaved species were amongst the six most adjacent trees. They conclude that this was partly due to a mixture effect, but that its effect-size was smaller relative to other factors (e.g. wet soils, recent harvest activity). Notably, and more generally, the evidence for a mixture effect *per se* is highly variable and often contradictory (Bauhus et al., 2017).

In summary, the evidence for a mixture effect remains too unclear (Bauhus et al., 2017; Jactel et al., 2017), to suggest that either an intimate, or a patch scale mixture of wind resistant (ie birch) and wind sensitive trees (ie spruce), would better reduce the probability of stand-level wind damage

3.4.2. Fire

We found no studies that addressed the spatial scale of a mixture on fire risk. More generally, the flammability of a forest stand depends on the availability of fuel and its distribution within a stand (Schelhaas et al., 2010), all of which is dependant on tree species composition and stand openness (Jactel et al., 2009). In general, conifer foliage is much more flammable than broadleaf foliage, due to its higher content of resins and oils (Bond and van Wilgen, 1996), which has implications for the potential to initiate and sustain a crown fire. Notably, in this region ground fires are the more common fire category. Trees influence ground fires through their litter characteristics (e.g. caloric value, flammability), and via canopy effects on the composition and cover of understory plant species. For example, in the conifer dominated stands of Eurasia, feathermosses (e.g. *Pleurozium, Hylocomium*) are the primary fuel source. In contrast, *Betula* spp. generally produce far less flammable litter, and is less associated with flammable understory vegetation. However, the higher leaf area index of spruce trees often results in denser darker stands that are less flammable than open stands, where sun and wind can dry out understory fuels. Furthermore, spruce needles are likely to be more compacted and less ventilated as fuel, compared to the leaf litter of *Betula* (Zhao et al., 2019).

Whether intimate or patch scale mixtures better suppress fire risk, will likely depend on the potential benefits of intimately mixing less flammable broadleaf trees throughout a stand, and their associated influences on the fuel bed, against the potential negative implications of higher insolation that increases the dryness and flammability of the understory. Rainfall, temperature, soil types, and stand density are important determinants, further limiting the potential to draw clear conclusions, especially in the absence of empirical studies.

3.4.3. Pathogens

In general, damage to trees from pathogens and associated epidemic events is often reduced in mixtures relative to monocultures, due to the more diverse tree species composition and structures, and the related decrease in pathogen transmission to susceptible hosts (Hantsch et al., 2014; Ostfeld et al., 2005). The spatial arrangement of the mixture may therefore influence the build-up of available pathogen propagules that have the potential to infect host trees. If the total density of host trees per area is reduced, this limits suitable substrate, which can dilute pathogen impacts (Civitello et al., 2015). A tree's capacity to defend itself against a specific pathogen can also be affected by the species of neighbouring trees, e.g. through inter- and intra-specific competition for resources (water, nutrients, light) (Bauhus et al., 2017; Huot et al., 2014). Likewise, the spatial structure of mixtures influences the abiotic microclimate within stands (Field et al., 2020), with potential consequences for pathogen propagation and transmission. For foliar and stem diseases, temperature, humidity and plant surface wetness are important for pathogen establishment, whereas solar radiation and air turbulence influence aboveground dispersal (DiLeo et al., 2014). The consequences of spatial-grain on pathogen damage also likely depends on the pathogen's dispersal mode (Prospero and Cleary, 2017), which can require direct contact between infected and healthy trees (e.g., root contacts), or occur over larger spatial scales via dispersal vectors (e.g., bark beetles) or wind (Ostfeld et al., 2005). If the pathogen relies on insect vectors, sparsely aggregated host trees in a mixture may be more difficult to locate, especially if the insects depend on host-specific volatile cues (Jactel et al., 2011).

With respect to spruce-birch mixtures, we did not find any studies that explicitly focus on spatial grain and pathogens. Spruce and birch are hosts to several pathogens, mainly fungi, some of which have potential to cause significant economic losses. amongst the most devastating is root and butt rot caused by *Heterobasidion* spp, which spreads secondarily via root contacts (Woodward, 1998). In the Nordic countries there are two species, *H. annosum,* which shows the widest host range, including spruce and birch, and *H. parviporum*, which is more specialized on Norway spruce. If a Norway spruce-birch mixture has only *H.*

parviporum present, then placing the birch to reduce intra-species root contacts may reduce spread (Piri et al., 1990). Although this may favour the use of intimate mixtures, empirical support is lacking. *Armillaria* is another important root pathogen capable of causing growth reduction or mortality. Several species of *Armillaria* (including *A. borealis, A. gallica, A. cepistipes* and the more aggressive *A. ostoyae*) are found in Scandinavia which spread by root-root contact and via rhizomorphs in the soil. North American studies indicate that damage can be reduced by using low susceptibility hosts to limit disease spread between the roots of susceptible hosts (Cleary et al., In process).

In summary, if the primary consideration is reducing damage to spruce from the economically important *H. parviporum*, then intimate mixtures may reduce the risk of spread via intra-species root contacts. However, targeted experimental studies testing the impact of mixture design on pathogen damage are needed, especially as the trajectories of tree-pathogen interactions are highly species-specific and environmentally dependant.

3.4.4. Pest insects

The effect of mixtures on insect herbivory damage varies, depending in-part on the tree and insect species in question. Specifically, tree species diversity may decrease the abundance of specialist insect herbivores, and thus reduce the damage to a focal plant (associational resistance hypothesis); or increase damage by populations of generalist herbivores (associational susceptibility hypothesis). Increasing tree diversity may also sustain a higher abundance and diversity of generalist predators of pest insects, by better providing alternative prey sources (natural enemy hypothesis). From both perspectives, mixed forests appear to be more resistant to insect pests than monocultures (Jactel et al., 2017; Vehvilainen et al., 2006), though studies from boreal forests are few.

The primary concern in spruce-dominated production stands are outbreaks of the specialist bark beetle *Ips typographus,* which causes extensive mortality of Norway spruce (Seidl et al., 2016). Studies using satellite imagery find that stand colonization risk increased with the volume of Norway spruce (Kärvemo et al., 2016), but correspondingly decreased once birch basal area exceeded 25 m^3 ha^{-1}. However, the impact on risk of increasing birch prevalence were small relative to the effect of absolute spruce volume. The benefits of adding birch to create spruce-birch mixtures derive from the volatiles released, which disturb the olfactory host-searching behaviour of bark beetles (associational resistance hypothesis), and thereby decreasing risk of bark beetle colonization (Kausrud et al., 2012; Schiebe et al., 2011). With respect to pest predators, intimate mixtures of birch may also improve ant predation rates of the pest species *Neodiprion sertifer* (Kaitaniemi et al., 2007), without adversely affecting more specialist parasitoid species (Bellone et al., 2020; Klapwijk and Björkman, 2018).

These results suggest that intimate mixtures may better dampen pest outbreaks through both reduced host tree colonization, and consistently higher predation pressure. However, generalists may still benefit from the presence of multiple hosts (Jactel et al., 2017). More research is thus needed into the temporal and spatial variation of damage patterns in mixtures to test this conjecture.

3.4.5. Cervid browsing

We found no studies contrasting browsing damage to birch or spruce caused by cervids in relation to patch versus intimate mixtures, but inferences can be made from theory and a few relevant field studies. In terms of cervid foraging damage in mixtures, spruce is far less likely to be consumed compared to birch (see "Cervid game"). However, both are at risk of browsing damage when young and within browsing height (Bergquist et al., 2010; Bergqvist et al., 2014). The attractant-decoy hypothesis (Atsatt and O'Dowd, 1976) proposes that a plant may be protected from browsing if growing close to a more selected plant. Under this hypothesis, spruce trees in an intimate mixture with birch could be less susceptible to damage than spruce in a patch mixture. Because

higher densities of birch biomass (i.e. patches) are preferably browsed by moose (Wam and Hjeljord, 2010) (and possibly other cervids), an intimate mixture could also limit damage to the birch. For these reasons, it is possible that intimate mixtures may result in lower damage levels to production stems during stand regeneration, when damage is most often caused (Bergquist et al., 2019).

Spruce is also susceptible to browsing damage later in the rotation, as red deer and moose sometimes eat the bark of mature spruce stems (Jarnemo et al., 2014). Importantly, mature spruce stands with more forage on the forest floor are less bark damaged by deer than stands with a poor field layer (Jarnemo et al., 2014). In patch mixtures the understory vascular biomass and diversity will likely be higher than in intimate mixtures (see "Cervid game"), and for a longer period of the rotation (in intimate mixes, there is more shadowing by spruce with time). This beneficial outcome would be more prevalent in regions with limited snow fall, as winter is when most damage occurs. Importantly, the benefits of reduced damage from any spatial grain of mixtures must be adopted at landscape scales, as all cervids use home ranges far larger than the average stand size.

In summary, intimate mixtures may be beneficial for reducing browsing damage on both spruce and birch during early phases of the rotation, if only the stand scale is considered. In contrast, patch scale spruce-birch mixtures may be less prone to browsing damage (e.g. bark stripping of spruce) than intimate scale mixtures, during later phases of the rotation, primarily due to associated increases in understory food availability. A greater availability of alternative forage at the landscape scale would reduce damage levels overall, thus also favouring patch mixtures. Our conclusions are speculative and require further research.

4. Discussion

Our results provided two important findings. First, experts highlighted the pervasive lack of empirical studies for their fields that addressed scale-related issues in spruce-birch mixtures, making it difficult to confidently provide evidence-based guidance to forest owners, managers, and policy makers seeking to understand the influence of patch versus intimate scale mixtures on forest biodiversity and ecosystem service outcomes. Second, the limited evidence that is available, was however often deemed sufficient to tentatively tip the scales in favour of either patch or intimate scale mixtures, at least as informed hypotheses requiring further testing. The net result was a picture in which patch versus intimate spruce-birch mixtures may well provide their own distinct suite of biodiversity and ES benefits. Just as no single forest type is optimized for the delivery of all goods and services (Van der Plas et al., 2016), these results indicate that neither patch nor intimate scale mixtures will have a monopoly on positive outcomes across the biodiversity and ES categories assessed. Instead, while patch scale mixtures were associated with positive outcomes for biodiversity (with the possible exception of bryophytes), cervid game and harvesting costs, intimate mixtures had the potential to reduce pathogen and pest damage, and perhaps even benefit production outcomes (Fig. 2).

What is notable in these results is the uneven potential distribution of benefits associated with intimate and patch scale mixtures. Whereas patch scale mixtures were thought to benefit most taxa in the biodiversity categories, intimate mixtures were associated with positive suggested outcomes for some biotic regulatory services. This result was not intuitive, as previous assessments have often identified synergistic outcomes with respect to biodiversity outcomes and a range of regulatory services; for example when contrasting monocultures and mixtures (Felton et al., 2016b; Huuskonen et al., 2021). Our results instead provide clear motivation to test whether the finer spatial scale resolutions occurring within some mixture combinations, results in potential trade-offs between optimizing tree placement for biodiversity, versus reducing the risks associated with e.g. pest and pathogen damage. In contrast, we also identified potential synergies provided by intimate mixtures, with respect to reduced risks pest and pathogen damage, and the
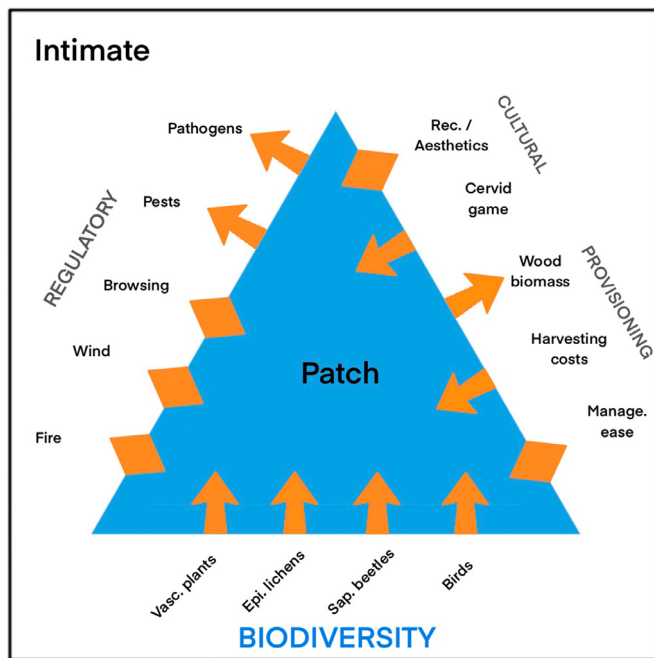
Fig. 2. Summary diagram illustrating the direction in which experts hypothesized the balance of drivers leaned with respect to favouring patch or intimate scale spruce–birch mixtures in terms of biodiversity, provisioning, regulatory (reduced risk of damage), and cultural services. Outward arrows favour intimate scale mixtures, whereas inward arrows favour patch scale mixtures for the topic assessed. The diamond shape is used where theory and scientific evidence is too limited or inconsistent to draw even an informed hypothesis favouring either alternative, or is otherwise neutral in terms of outcomes.

potential for improved production outcomes via increased tree growth rates (though financial benefits from increased growth may be overridden by harvesting costs). The key point is that uncertainties and potential trade-offs involving the spatial grain of the mix needs to be considered when discussing or conveying the expected contributions of mixed-forests to biodiversity and ecosystem service outcomes.

If the hypothesized potential drivers are important determinants of the biodiversity and ES outcomes assessed, then facilitating these processes will be key to ensuring that outcomes are realised. For example, almost all projected benefits from patch scale mixtures for biodiversity, were directly or indirectly associated with improved understory environmental conditions stemming from heterogeneous stand-level insolation improving habitat variation and niche diversity. The net result was the expected increased diversity of understory vascular plants, epiphytic lichens, saproxylic insects, and birds. Furthermore, the increased availability of understory forage in patch mixtures, could help reduce the risk of browsing damage by cervids, if applied at landscape scales. Management practices acting in opposition to a rich understory vascular plant community, would correspondingly negate many of the hypothesized biodiversity benefits of patch scale mixtures. For example, if stand density is too high, and patch sizes too small, this may largely negate any expected contribution of birches to understory insolation (Hedwall et al., 2019). Likewise, the contribution of patch-scale mixtures to saproxylic beetle diversity is nullified in the absence of adequate coarse woody debris (Jonsson et al., 2016), and the contribution of patch scale mixtures to epiphytic lichen diversity is strongly curtailed if rotation lengths are shortened (Dettki and Esseen, 2003).

Related caveats can be made when inferring the potential benefits of intimate mixtures to some biotic regulatory services. For example, it cannot be assumed that a stand possessing enough birch to classify as a mixture, or that ensuring this birch is dispersed throughout the stand, will limit damage by root rot or spruce bark beetle. Instead, a sufficient

proportion of birch will be needed to minimise spruce-spruce root contact and *H. parviporum* spread, just as sufficient densities of volatile releasing birches will be needed to effectively disturb the olfactory host-searching of spruce-bark beetles. The key point is that the extent to which these benefits can be achieved, depends on the extent to which the underlying inferred drivers are promoted, and related caveats addressed, beyond that dictated by the mixture scale adopted.

Across the biodiversity and ES topics assessed, the strongest empirical evidence was reserved for how the prevalence of birch in the overstory was likely to affect understory vascular plants (Hedwall et al., 2019). All other conclusions were primarily built on expert inference from theory, modelling, and indirectly relevant studies, rather than direct empirical support. In several cases, current knowledge was too limited, inconsistent or context dependant, to even tentatively infer outcomes, and the implications of patch vs intimate mixtures could therefore not be distinguished, if in-fact such responses occur at all. For example, despite knowledge that variation, openness and light are important determinants of people's preferences for forest environments for recreation (Filyushkina et al., 2017; Gundersen and Frivold, 2008), no studies were available that clarified whether patch or intimate mixtures would best match these reported preferences. In terms of production outcomes, further studies are needed to tease out the extent to which over-yielding effects may occur in spruce-birch mixtures, and more specifically, if such outcomes are in-fact enhanced by intimate mixtures. For some topics, the uncertainties stemmed not just from a lack of relevant scientific studies, but also from the large number of context-specific determinants of outcomes. For example, with respect to fire risk, outcomes depended on variables ranging from stand density to regional climate, whereas for "management ease", outcomes depended on the balance between the silvicultural treatments employed and resultant harvesting logistics. In addition, in some cases the extent of any projected benefit may be overridden by other factors. For instance, a reduction of cervid browsing damage following the increased availability of understory forage is realistic as long as the local cervid population size is not allowed to increase sufficiently (as managed by hunting quotas) to override such benefits. All of these uncertainties act as obstacles to evidence-based decision making. Targeted research efforts are therefore needed to overcome these obstacles, and in the interim, we caution against generalizing from mixture studies that do not caveat or control for mixture-scale.

5. Conclusion

Our results highlight the importance of actively investigating the influence of tree spatial arrangement when discussing the capacity of mixtures to help achieve production forest biodiversity and ES goals. Our preliminary findings suggest that either patch or intimate mixtures could eventually be advocated based on their own suite of costs, benefits, and risks (Fig. 1), with the specific conclusions reached dependant on the values stakeholders' place on different ecosystem goods and services. We emphasize however that what we provide here are informed hypotheses requiring further testing, and that the paucity of directly relevant studies prevented us from drawing firm conclusions for almost all topics addressed. The need to fill these knowledge gaps is urgent, as the type of mixture adopted has the apparent potential to invoke trade-offs between the contribution of production forests to biodiversity loss, and their capacity to both mitigate and adapt to accelerating anthropogenic climate change. We therefore hope our findings help to shine a light on these issues, and motive the targeted research needed to resolve the many remaining questions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

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