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Histoire des feux, dynamique de la végétation et variabilité climatique de l'Holocène en République de Komi

Chéïma Barhoumi

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

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Histoire des feux, dynamique de la végétation et variabilité climatique de l'Holocène en République de Komi

Présentée par Chéïma BARHOUMI

Le 18 novembre 2019

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AVANT-PROPOS

Cette thèse est présentée sous un format de type « articles » : elle est constituée d'une introduction générale (Chapitre I) puis de trois chapitres correspondant à trois articles scientifiques focalisés sur des objectifs/problématiques de recherche différents mais complémentaires de cette thèse. Le chapitre II (publié en 2019 dans « The Holocene ») a pour objectif de documenter l'histoire des feux en République de Komi au cours de l'Holocène. Le chapitre III (accepté dans « Journal of Biogeography », en cours de révision) vise à analyser la dynamique de la végétation de la République de Komi au cours de l'Holocène. Le chapitre IV (à soumettre dans « Climate of the Past ») a pour objectif de retracer l'évolution du climat de l'Holocène en République de Komi, et de quantifier les paramètres climatiques par une approche multi-proxies basée sur l'étude des grains de pollen et des biomarqueurs moléculaires de type branched Glycerol Dialkyl Glycerol Tetraethers (brGDGTs). Le chapitre V permet de synthétiser les résultats établis dans les chapitres précédents et, à la lumière de cette étude, de fournir des éléments de réponse aux problématiques soulevées dans le cadre de cette thèse. Le fait d'avoir privilégié le format sous article induit nécessairement certaines répétitions à travers les différents chapitres (zones d'étude, modèles d'âge, etc.), puisque la publication des articles induit leur indépendance. Les annexes de chaque article se trouvent à la fin des chapitres correspondant. Le plan général de la thèse est le suivant :

Chapitre I : Introduction générale

Chapitre II : Barhoumi, C., Peyron, O., Joannin, S., Subetto, D., Kryshen, A., Drobyshev, I., Girardin, M.P., Brossier, B., Paradis, L., Pastor, T. and Ali A. A. (2019). Gradually increasing forest fire activity during the Holocene in the northern Ural region (Komi Republic, Russia). *The Holocene* 0959683619865593.

Chapitre III : Barhoumi C., Ali A. A., Peyron O., Dugerdil L., Borisova O., Golubeva Y., Subetto D., Kryshen A., Drobyshev I., Ryzhkova N. and Joannin S. Did long-term fire control the coniferous boreal forest composition of northern Ural region (Komi Republic, Russia)? *Journal Of Biogeography*, accepté avec corrections majeures, en cours de revision.

Chapitre IV : Barhoumi C., Joannin S, Ali A. A., Ménot G., Golubeva Y., Subetto D., Kryshen A., Drobyshev I. and Peyron, O. Climate, vegetation and fire interactions in Northern Urals (Komi Republic, Russia) during the Holocene: a multi-proxy approach. *Climate of the Past*, à soumettre.

Chapitre V : Synthèse sur les relations entre le feu, la végétation et le climat au cours de l'Holocène en République de Komi et comparaison de la dynamique de feux de la Carélie, la République de Komi et la région du Lac Baïkal, à soumettre.

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LISTE DES ABREVIATIONS

AD	Anno Domini, an 0 de l'ère chrétienne
AMOC	Composantes de courants de surface et de profondeur de l'océan Atlantique A(tlantic meridional overturning circulation)
AO	Oscillation arctique (Arctic Oscillation)
C	Carbone
cal. yr BP	années calibrées avant le présent (calibrated years Before Present), le présent débutant en 1950 de notre ère.
CHAR	Taux d'accumulation de charbons
FRI	Intervalle de retour de feu (Fire Return Interval), nombre d'années entre deux évènements de feu consécutifs
brGDGTs	Branched Glycerol Dialkyl Glycerol Tetraethers
HTM	Optimum thermique Holocène (Holocene Thermal Maximum)
LGM	Dernier maximum glaciaire, il y a environ 21000 ans (Last Glacial Maximum)
MAT	Technique des analogues modernes ou des meilleurs analogues (Modern Analogue Technique)
NAO	Oscillation nord-atlantique (North Atlantic Oscillation)
PPE	Estimation de la productivité pollinique (Pollen Productivity Estimation)
SH	Anticyclone de Sibérie (Siberian High)
REVEALS	Estimations régionales de l'abondance de la végétation (Regional Estimates of Vegetation Abundance from Large Sites)
UB	Blocage de l'Oural (Ural Blocking)
WAPLS	Régression moyenne pondérée par les moindres carrés partiels (Weighted Averaged Partial Least-Squares regression)

RESUME DE LA THESE

Le changement climatique en cours entraîne et va continuer d'entraîner d'importantes modifications au niveau de la structuration et de la biodiversité des écosystèmes forestiers. Les forêts boréales, qui comptent parmi les plus grands biomes forestiers de la planète (32% du couvert forestier mondial), sont particulièrement impactées par de tels changements. Les incendies y sont des perturbateurs écologiques majeures et participent à la dynamique de ces forêts. Afin de mieux comprendre les mécanismes sous-jacents au fonctionnement de ces écosystèmes, et afin de mieux anticiper les changements encore à venir, l'étude de sa dynamique passée permet d'apporter des éléments de réponses en ce qui concerne les interactions feu-végétation-climat. L'objectif de la thèse consiste à étudier et à comprendre les interactions entre la dynamique des incendies, de la végétation et du climat au cours de l'Holocène (derniers 11700 ans) en République de Komi, une région de Russie, où ces questions ont jusqu'ici été très peu documentées. Dans un premier temps, l'étude de la dynamique des incendies a révélé que la fréquence des feux a augmenté de manière graduelle tout au long de l'Holocène. Les changements de végétation au cours de l'Holocène ont été retracés à partir de l'analyse des grains de pollen et du modèle REVEALS. Une forêt de type taïga claire (caractérisée par une majorité de *Pinus sylvestris* et *Betula* spp. et des feux de surfaces) s'est développée au début de l'Holocène, de 10000 à 6000 cal. yr BP. Ensuite, de 6000 à 3500 cal. yr BP, une taïga sombre s'est installée. Puis à partir de 3500 cal. yr BP, on observe le retour progressif de la taïga claire. Les reconstitutions paléoclimatiques basées sur une double approche, *via* l'étude des grains de pollen et des biomarqueurs moléculaires branched Glycerol Dialkyl Glycerol Tetraethers (brGDGTs), ont mis en évidence un optimum climatique entre 7000 et 4000 cal. yr BP. La mise en relation de ces résultats les uns avec les autres nous a amené à conclure que pour la première moitié de l'Holocène, le climat a eu une influence majeure sur la végétation. Puis à partir de 3500 cal. yr BP, le passage de la fréquence des feux sous une valeur seuil (FRI, Intervalle de retour de feu < 200 ans) a eu un impact plus fort que le climat sur la végétation. Depuis les 600 dernières années, l'intensification des activités humaines a mené à une surexploitation de la forêt et à une augmentation de l'activité de feu. Un autre aspect de la thèse a consisté à étudier les dynamiques des incendies de deux autres régions de Russie, en Carélie et dans la région sud du Lac Baïkal. La dynamique des feux y a été plus complexe qu'en République de Komi, car elle n'a pas suivi la même tendance de décroissance graduelle et continue du FRI.

Mots-clefs : Feu, forêt boréale, Holocène, Russie, charbon, reconstruction des températures issues des grains de pollen, GDGTs, REVEALS

ABSTRACT

Ongoing climate change is causing and will continue to generate significant changes in the structure and biodiversity of forest ecosystems. Boreal forests, which are among the world's largest forest biomes (32% of the world's forest cover), are particularly affected by such changes. Fires are major disturbances and contribute to the dynamics of these forests. In order to better understand the mechanisms underlying the functioning of this type of forest, and to anticipate future changes, the study of its past dynamics allows us to provide some answers regarding the link between fire, vegetation and climate. The aim of this PhD is to study and understand the interactions between the dynamics of fire, vegetation and climate during the Holocene (last 11700 years) in the Republic of Komi, a region of Russia, where these questions have been poorly documented. Vegetation dynamics during the Holocene were reconstructed from pollen grain analysis and the REVEALS model. A light taiga forest (characterised by *Pinus sylvestris* and *Betula* spp, associated with surface fires) developed in the early Holocene, from 10,000 to 6,000 cal. yr BP. Then, from 6000 to 3500 cal. yr BP, a dark taiga settled. Then from 3500 cal. yr BP, we observe the gradual return of the light taiga. Paleoclimatic reconstructions based on a multi-proxy approach, pollen grains and molecular biomarkers branched Glycerol Dialkyl Glycerol Tetraethers (brGDGTs) studies, have shown a climatic optimum between 7000 and 4000 cal. yr BP. The relationship between these results led us to conclude that for the first half of the Holocene, climate had a major influence on vegetation. Then from 3500 cal. yr BP, the change in fire frequency below a threshold value (FRI, Fire Return Interval < 200 years) had a greater impact on vegetation than the climate. Over the past 600 years, the intensification of human activities led to overexploitation of the forest and an increase in its fire activity. Another aspect of the PhD was the study of the fire dynamics for two other regions of Russia, in Karelia and in the southern region of Lake Baikal. Fire dynamics were more complex than in the Republic of Komi, as they did not follow the same trend of gradual decline in the FRI.

Keywords: Fire, boreal forest, Holocene, Russia, pollen-inferred temperatures, GDGTs, REVEALS

Chapitre I.

INTRODUCTION GENERALE

Le changement climatique en cours entraîne et va entraîner encore d'importantes modifications au niveau de la structuration et de la biodiversité des écosystèmes (Team et al., 2014; Nolan et al., 2018). La forêt boréale, bien que peu diversifiée, compte parmi les plus grands biomes forestiers de la planète (32% du couvert forestier mondiale). Son étendue et son fonctionnement sont particulièrement impactés par de tels changements (Weber and Flannigan, 1997; Blarquez et al., 2015; Hoegh - Guldberg et al., 2018). Cet écosystème se situe dans l'hémisphère Nord et s'étend non seulement en Eurasie, sur les territoires de la Russie et de la Fennoscandie, mais aussi au Canada et aux Etats-Unis, en Amérique du Nord (Figure I.1) (Gorham, 1991; Kneeshaw et al., 2011; Goldammer, 2015). Appelée « taïga » pour la partie Eurasienne, la forêt boréale s'y étend sur 17 millions de km². Elle stocke environ 20% du carbone (C) du globe dans ses tourbières, par lente accumulation de matière organique du sol et des arbres et de charbon depuis le dernier maximum glaciaire, il y a 21000 ans (Zoltai et al., 1998; Vygodskaya et al., 2007; Kneeshaw et al., 2011; Pan et al., 2011; Pflugmacher et al., 2011; van Bellen et al., 2012; Brandt et al., 2013). Les arbres qui sont les plus représentées dans ce biome sont les conifères, principalement les pins (*Pinus banksiana*, *Pinus sylvestris*, *Pinus sibirica*, *Pinus* spp.), mais aussi les mélèzes (*Larix* spp.), les épicéas (*Picea* spp.), les sapins (*Abies* spp.). En ce qui concerne les feuillus, les principales espèces sont les bouleaux (*Betula* spp.), les peupliers (*Populus* spp.) et les aulnes (*Alnus* spp.) (les taxons identifiés au genre sont représentés par l'adjectif « spp. ») (Goldammer and Furyaev, 1996).

Dans les forêts boréales, les incendies déclenchés par la foudre ou par l'Homme ont un impact majeur sur les dynamiques de la végétation, de la biodiversité et des sols (Blarquez et al., 2015; Kaplan et al., 2016). La récente augmentation des activités de feux dans ces écosystèmes, constatée par télédétection soulève des questions d'ordre écologique et socio-économique (Naryshkin, 2003; Marlon et al., 2016; Shuman et al., 2017), notamment au regard des nombreux services écosystémiques qui y sont associés, tels que la production de bois, la purification de l'eau ou la limitation de l'érosion des sols (Gauthier et al., 2015). Le climat a également un rôle considérable sur la dynamique de la forêt boréale. En effet, les changements climatiques qui ont eu lieu depuis la fin de l'ère glaciaire, puis au cours de l'Holocène (derniers 11700 ans) sont responsables de la migration des espèces (Goldammer and Furyaev, 1996). Les conséquences du réchauffement climatique sont déjà observées dans ces régions, notamment au Canada et en Russie, où des hivers et des printemps plus chauds (augmentation de 2 à 3°C) ont été enregistrés depuis les années 1960 (Stocks et al., 1998). De plus, le changement climatique en cours a un impact sur le bilan net du stockage de C puisque l'augmentation des

températures actuelles va augmenter l'émission de C dans l'atmosphère (Gorham, 1991), notamment *via* la combustion du C séquestrés dans les sols et tourbières. Ajoutons à cela que l'exploitation par rotation courte des forêts boréales semble maintenant faire passer ce biome d'un état de puit de C à celui de source de C (Walker et al. 2019).

En terme de répartition spatiale, à l'heure actuelle, plus de 70% du couvert de la forêt boréale se situe en Eurasie, et majoritairement en Russie (Goldammer and Furyaev, 1996), où elle s'étend sur 1.181 millions d'hectares (Goldammer and Furyaev, 1996). La forêt boréale eurasiennne se divise en deux types de forêts, la taïga sombre (ou « dark taïga ») et la taïga claire (« light taïga »). La taïga sombre est majoritairement composée d'espèces peu adaptée aux incendies, telles que *Picea* spp. (*Picea obovata* et *Picea abies*), *Pinus sibirica* et *Abies sibirica*, tandis que la taïga claire est dominée par des espèces adaptées, dites « résistantes » au feu et dont le cycle de vie en est dépendant, comme *Pinus sylvestris*, *Larix* spp. et *Betula* spp. (Lapenis et al., 2005; Schulze et al., 2005; Shorohova et al., 2009; Goldammer, 2015).

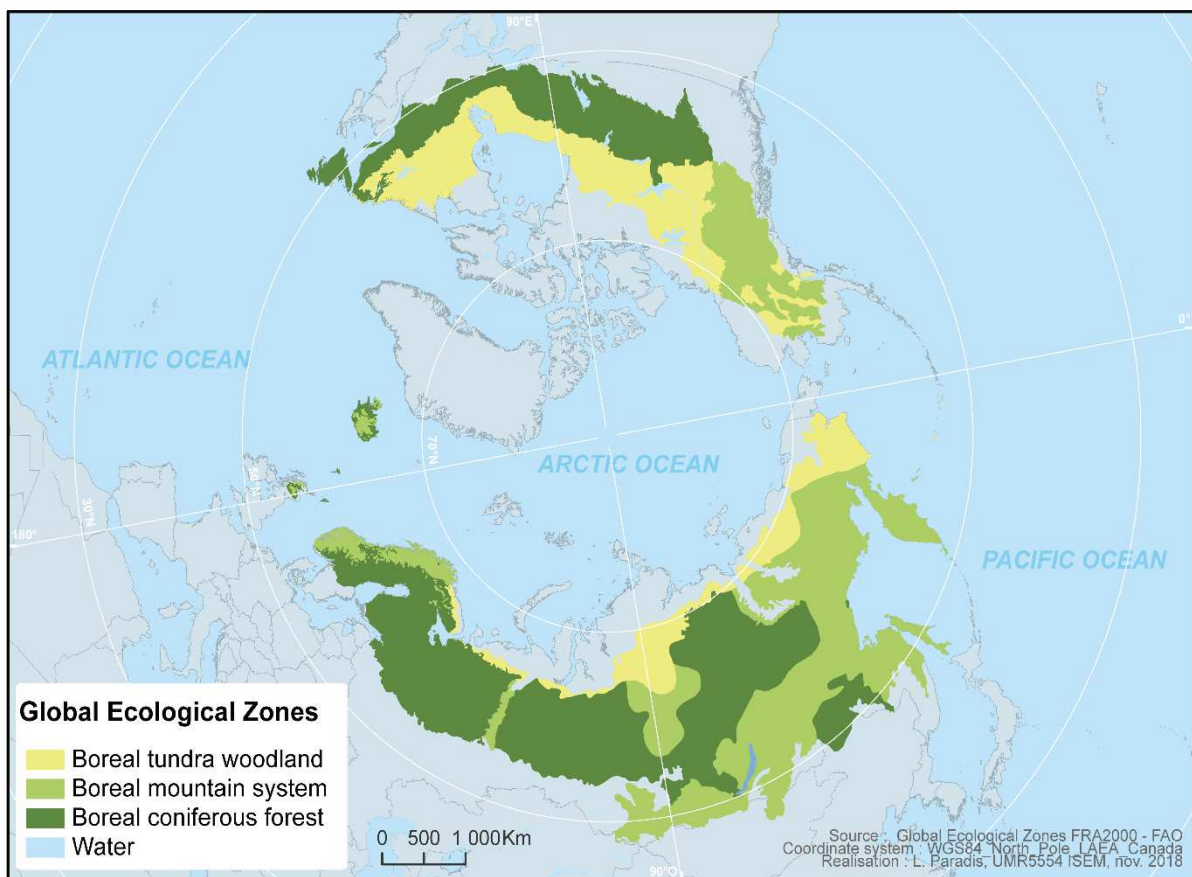


Figure I.1 : Carte de la répartition actuelle des forêts boréales sur Terre

1. 1. INTERACTIONS FEUX-VEGETATION-CLIMAT DANS LES ECOSYSTEMES BOREAUX

1.1.1. Généralités

Dans le contexte du changement climatique, l'augmentation et l'intensification des épisodes de sécheresse pourraient générer une modification de la dynamique des feux dans les forêts boréales (Goldammer and Furyaev, 1996). Une augmentation de l'activité de feu (en terme de fréquence, mais aussi de sévérité, avec des incendies plus intenses) est attendue, avec pour conséquences un rajeunissement des populations d'arbres, mais également une diminution du stockage de C par ceux-ci (Stocks et al., 1998) (Figure I.2). Des changements dans la dynamique de la végétation pourraient également résulter du changement de la dynamique des feux et du remplacement progressif des espèces de conifères par des espèces feuillues (Goldammer and Furyaev, 1996). Cependant, les prédictions des modèles concernant la dynamique de la forêt boréale et des feux qui en dépendent dans le contexte du changement climatique sont toujours sujettes à controverses (Randerson et al., 2006). En effet, la végétation, le climat et les incendies changent en interagissant les uns avec les autres, rendant complexe la compréhension de la chaîne causale (Randerson et al., 2006). Les études paléoécologiques, qui font le lien entre les changements du climat, de la végétation et des incendies au cours du temps retracent ces interactions étroites. Elles permettent d'apporter un éclairage nouveau sur des intervalles de temps particulièrement pertinents à l'échelle de la vie des arbres (jusqu'à 400 ans pour *Picea* sp., selon Gromtsev, 2002) et des successions végétales. Cette approche permet d'améliorer la compréhension de ces mécanismes complexes, en particulier au cours de l'Holocène (Randerson et al., 2006; Power et al., 2008; Girardin et al., 2009). De telles études ont été menées au Canada, en Alaska et également en Fennoscandie et au Danemark (e.g. Hu et al., 2006; Girardin et al., 2009, 2013; Clear et al., 2014) et pour des périodes de temps plus anciennes comme le Pliocène (Fletcher et al., 2019). Les travaux menés en Amérique du nord montrent que la fin de l'Holocène était moins favorable aux incendies de forêt (Hély et al., 2010; Ali et al., 2012). Plus précisément, durant les 3000 dernières années, le climat qui est devenu plus froid et plus humide a provoqué une diminution de la fréquence des feux au sein de la forêt boréale (Ali et al., 2012). Les données obtenues montrent également que la longueur de la saison de feux a fortement diminué à partir de 3000 cal. BP (Hély et al., 2010). Cette diminution de la longueur de la saison de feu est corrélée à la diminution graduelle de

l'insolation estivale (juillet et août) et à l'augmentation des précipitations annuelles (Hély et al., 2010; Ali et al., 2012). D'autres travaux ont montré que les liens entre le climat et les feux n'étaient pas toujours directs : par exemple en Alaska, une augmentation de l'activité de feu a été observée au cours de l'Holocène, en même temps que la mise en place d'un climat plus humide et plus froid (Hu et al., 2006). Cependant, durant cette période, l'expansion de *Picea mariana*, une espèce très inflammable explique l'augmentation de l'activité de feu (Hu et al., 2006). En Fennoscandie et au Danemark, une autre étude a mis en évidence l'impact de la végétation sur la dynamique des incendies, par l'expansion de *Picea abies*, espèce dite sensible aux incendies et qui associée à une faible activité de feu (biomasse brûlée) (Clear et al., 2014). L'ensemble de ces travaux met en évidence le fait que **les relations climat-feu-végétation sont complexes, et nécessitent le développement de travaux de recherche retraçant ces interactions à différentes échelles d'espace et de temps.**

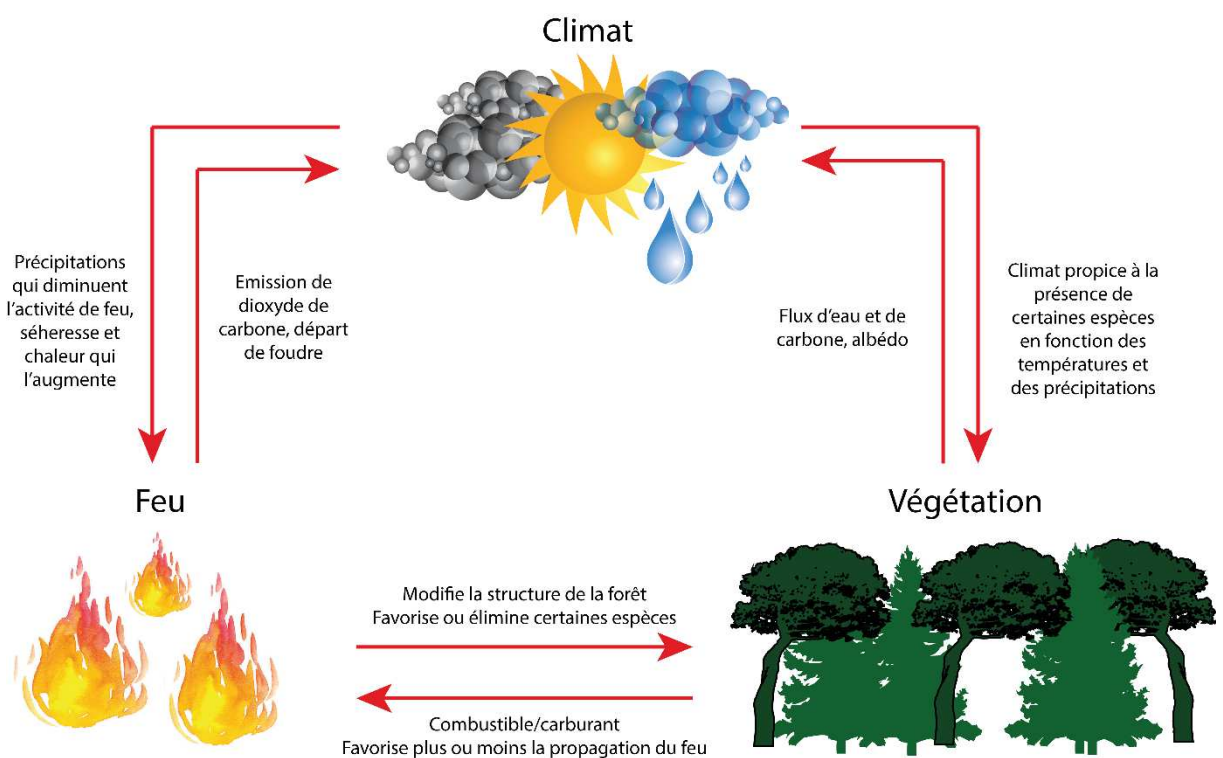


Figure I.2 : Schéma simplifié des interactions entre le climat, le feu et la végétation dans les écosystèmes boréaux

1.1.2. La taïga Eurasienne

Contrairement à l'Amérique du Nord, la Russie est une région peu documentée en ce qui concerne l'activité de feux passés et les mécanismes qui les relie au climat et à la dynamique de végétation. Pourtant, à l'heure actuelle, c'est une région qui recense annuellement de nombreux feux (entre 10000 et 30000, relevés dans les aires protégées (Goldammer and Furyaev, 1996)). L'activité de feu est particulièrement importante dans la région de Sibérie (Goldammer, 2015). Le régime des feux diffère en fonction du type de taïga. En général, la taïga sombre est associée à des feux de faible fréquence, car les espèces qui la composent sont sensibles aux incendies. Cependant lorsque les incendies se produisent, ils sont intenses et sont des feux de type couronne, brûlant les arbres jusqu'à la cime et étant généralement meurtriers (Schulze et al., 2005). La taïga claire est associée à des incendies qui ont une fréquence élevée, mais de faible intensité, caractérisés par des feux de surface, qui ne brûlent que la partie basse des troncs d'arbres et étant en général non meurtriers pour les arbres qu'ils touchent (Schulze et al., 2005). Les espèces qui composent la taïga claire sont stimulées par les incendies, qui sont bénéfiques dans leur cycle de vie (Goldammer and Furyaev, 1996), (Tableau I.1). Mais commençons tout d'abord par rappeler le contexte climatique dont sont héritées les taïgas eurasiennes.

1.1.3. Contexte climatique

De par la taille de ce continent, les régions d'Eurasie répondent différemment aux grandes tendances climatiques. En effet, durant le dernier maximum glaciaire (21000 cal. yr BP), seul le Nord-Ouest européen de la Russie a été recouvert par des calottes glaciaires (Svendsen et al., 2004) (Figure I.3), contrairement à l'Amérique du Nord qui était presque complètement recouvert d'Ouest en Est (Clark et al., 2009). Au cours du Tardiglaciaire (14700 cal. yr BP), le climat s'est rapidement réchauffé avec des oscillations climatiques rapides. L'Holocène est une période climatiquement stable, qui correspond à l'Interglaciaire actuel. Des études sur la Russie du Nord-Ouest ont montré que la première moitié de l'Holocène a été sujette à un réchauffement général des températures, en partie dû à l'impact de l'insolation et du système de circulation océan-atmosphère Nord-Atlantique (Kultti et al., 2003; Väliiranta et al., 2003). Ensuite, à partir du milieu de l'Holocène (vers 5500 cal. yr BP), les conditions de températures se sont dégradées, et les précipitations ont augmentées, entrecoupées par une

période de réchauffement à 2000 cal. yr BP (Kultti et al., 2003; Seppä et al., 2009a). Plus à l'Est, en Sibérie, une période de réchauffement a également été enregistrée au début de l'Holocène, entre 10000 et 7000 cal. yr BP, liée à une forte insolation, suivie d'une période de détérioration des conditions climatiques de 6500 à 5000 cal. yr BP, avant une nouvelle augmentation des températures à partir de 5000 cal. yr BP, qui peut être expliquée par les effets combinés de la réduction de la glace de mer, de l'augmentation de l'activité cyclonique le long du front polaire, et de l'affaiblissement de l'anticyclone sibérien (Tarasov et al., 2007).

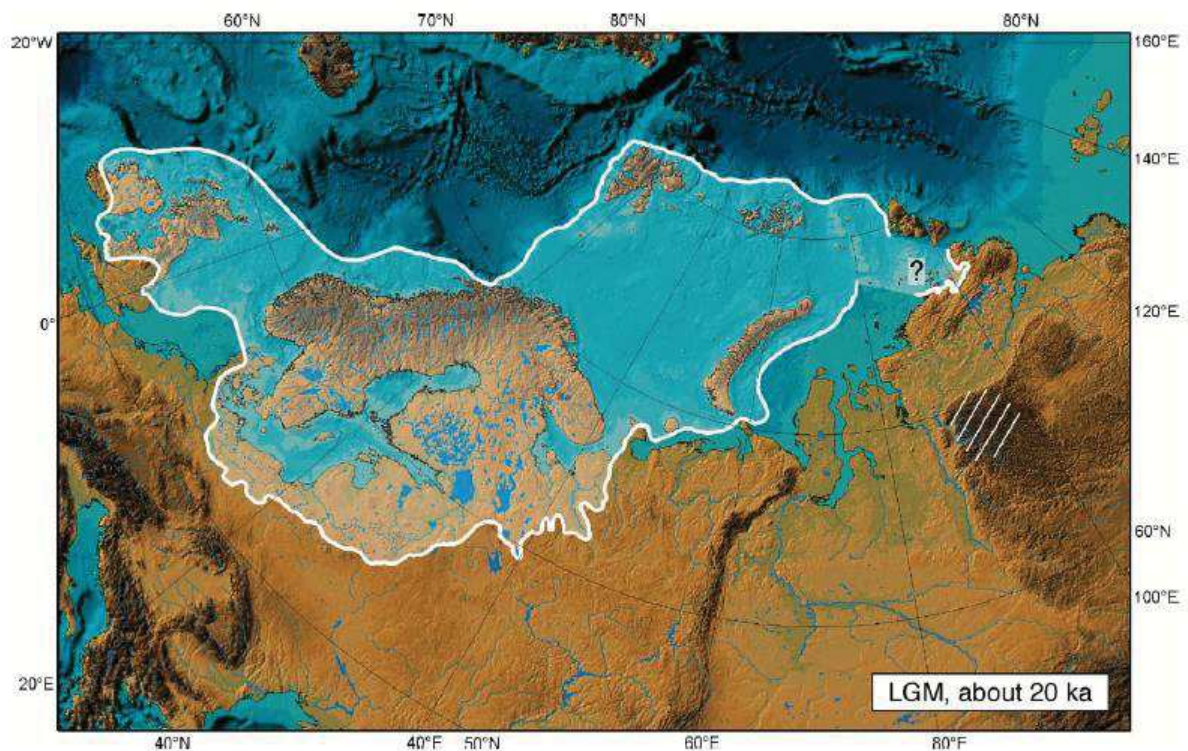


Figure I.3 : Extension du glacier du dernier maximum glaciaire en Eurasie, il y a environ 21000 ans, d'après Svendsen et al., (2004)

1.1.4. L'écologie des taxons boréaux

Le réchauffement caractéristique du début de l'Holocène a permis la mise en place de la forêt boréale et l'installation des espèces qui la constitue. Des zones refuges ont pu permettre le maintien d'individus de certaines espèces, au-delà de leur aire limite de répartition et ont pu permettre à ces population de se développer lorsque les conditions climatiques se sont montrées plus favorables (Gervais et al., 2002). Ainsi, des espèces pionnières comme *Pinus sylvestris* et

Betula spp. ont pu se développer rapidement. *Pinus sylvestris* est un taxon eurythermique (Tableau 1.1), capable de supporter de grandes amplitudes des températures et dont la répartition actuelle s'étend à toute l'Europe (Farjon, 2010). Il est caractéristique des taïga claires, tout comme *Betula* spp., car il est adapté aux incendies fréquents (s'adapte à des valeurs de FRI, Intervalle de retour de feu : nombre d'année entre deux évènements de feu consécutifs très faibles, autour de 30 à 40 ans) grâce à l'auto-élagage (ses branches basses tombent et ne permettent ainsi pas au feu de se propager vers sa cime), et grâce aussi à une écorce très épaisse. De plus le passage d'un feu permet l'amélioration des conditions de germination des graines de *Pinus sylvestris* (Goldammer and Furyaev, 1996). Un autre taxon caractéristique des forêts boréales de Russie est *Picea* spp. (*Picea abies* au niveau de la Russie européenne et *Picea obovata* au niveau de la Sibérie (Giesecke and Bennett, 2004; Schulze et al., 2005; Bezrukova et al., 2013). *Picea* spp. est également une espèce eurythermique (Tableau 1.1) et lorsqu'elle est le taxon dominant au sein d'une forêt, celle-ci est alors plutôt caractéristique d'une taïga sombre (Goldammer and Furyaev, 1996). *Picea abies* a lentement colonisé les forêts boréales en Eurasie dès le début de l'Holocène, par le Nord-Ouest de la Russie lorsque les populations de *Picea obovata* sont restées présentes en Sibérie (c'est-à-dire à l'Est du continent) au cours du LGM (dernier maximum glaciaire, il y a environ 21000 ans) puis se sont développées vers l'Ouest (Giesecke and Bennett, 2004; Tollefsrud et al., 2015; Tsuda et al., 2016). Les deux espèces se sont hybridées au cours de l'Holocène dans la région de la République de Komi (Tollefsrud et al., 2015). *Picea* spp. ne tolère pas les incendies, tout comme *Abies sibirica* et *Pinus sibirica*, qui forment la taïga sombre (Goldammer and Furyaev, 1996). C'est pourquoi ces espèces ne peuvent s'établir que lorsque le FRI est élevé, avec des valeurs supérieures à 200 ans, qui permettent ainsi à l'arbre de croître jusqu'à sa maturité sexuelle (jusqu'à 200-300 ans) pour générer des graines, ce qui peut arriver à un âge avancé de l'arbre, notamment pour *Pinus sibirica* (Goldammer and Furyaev, 1996; Kharuk et al., 2009).

Tableau I.1 : Caractéristiques écologiques des principaux taxons des forêts boréales de Russie, synthétisées depuis (Sannikov and Goldammer, 1996; Schulze et al., 2005; Semerikova et al., 2011 ; Goldammer, 2015)

	<i>Taïga claire</i>		<i>Taïga sombre</i>		
	<i>Pinus sylvestris</i>	<i>Betula spp.</i>	<i>Abies sibirica</i>	<i>Pinus sibirica</i>	<i>Picea spp.</i>
LGM	Zones refuges en Europe et zones refuges cryptiques en Russie	A continué de se développer pendant le LGM en Russie	A continué de se développer pendant le LGM en Sibérie (à l'Est de la Rep. de Komi)	A continué de se développer pendant le LGM en Sibérie (à l'Est de la Rep. de Komi)	Zones refuges en Europe (<i>Picea abies</i>) et en Sibérie (<i>Picea obovata</i>)
Conditions de développement	Espèce pionnière	Espèce pionnière	Espèce de fin de succession	Espèce de fin de succession	Espèce à la fois pionnière et de fin de succession
Conditions d'humidité	Favorisé par des sols secs	Ubiquiste	Favorisé par des conditions humides (précipitations de 800 à 900 mm/an)	Favorisé par des conditions humides (précipitations de 800 à 900 mm/an)	Favorisé par des conditions humides (précipitations de 800 à 900 mm/an.
Type de sol	Sols secs et sableux, acidophile	Acidophile	Acidophile	Milieus humides très déterminants, acidophile	Plaines inondables et près des cours d'eau Ne supporte pas les inondations, acidophile
Températures / permafrost	Espèce eurithermique	Espèce eurithermique	Ne supporte pas les hivers trop longs et les sols gelés		Besoin de températures froides et de sol neigeux épais en hiver Espèce eurithermique
Feux (dont FRI)	Espèce pyrophyte Meilleure résistance pour les arbres de 20 à 40 ans. Stimulation par l'ouverture des graines/cônes par le feu. Feux de surfaces car auto-élagage de l'arbre. FRI : 30 à 40 ans	Re-paraît rapidement après des feux de surface même si tués par ceux-ci grâce à leurs racines (resprouting)	Feux de couronnes favorisés car feuillage très inflammable et branches permettent l'ascension du feu FRI : 200 à 300 ans	Feux de couronnes FRI : 200 à 300 ans	Feux de couronnes favorisés car feuillage très inflammable et branches permettent l'ascension du feu. FRI : 200 à 300 ans
Dispersion des graines	Dispersion par le vent	Dispersion par le vent et repousse des racines	Dispersion par le vent et repousse des racines	Dispersion par le biais du Geais de Sibérie. Production de graines de 30 à 40 ans parfois 140 à 160 voire 200	Dispersion par le vent

1.2. OBJECTIF DE LA THESE ET HYPOTHESES DE TRAVAIL

Cette thèse s'inscrit dans le cadre du projet de recherche international « PRERREAL » (Improving PREDictability of circumboREAL forest fire activity and its ecological and socio-economic impacts through multi-proxy data comparisons). C'est un projet financé de 2016 à 2020 par le programme international Belmont, qui implique des laboratoires de recherches de différents pays : Suède, France, Norvège, Pays-Bas, Chine, Canada, Finlande et Russie. Les objectifs de ce projet de recherche sont d'identifier les facteurs climatiques qui contrôlent l'activité des feux dans les régions boréales, afin d'être en mesure d'améliorer la fiabilité des prédictions du régime des feux futurs.

Dans ce contexte, l'objectif principal de cette thèse est de déterminer quelle fût l'histoire des feux au cours de l'Holocène dans plusieurs régions de Russie, et de comprendre les interactions climat-feu-végétation qui s'y déroulent. La Russie est un territoire très vaste, qui concentre la majorité de la forêt boréale eurasienne et ne présente pas les mêmes caractéristiques de climat et de végétation sur l'ensemble de sa surface. C'est un territoire à ce jour peu documenté en termes d'études paléoécologiques multi-proxies. C'est pourquoi, dans ce projet de thèse, trois zones d'études distinctes ont été définies au sein du territoire Russe :

- au Nord-Ouest, la région de la Russie européenne, avec l'étude de la Carélie, proche de la Fennoscandie.
- Au niveau de la région Ouest de l'Oural, en République de Komi, où une continentalité plus importante et un impact des montagnes de l'Oural sont attendus sur la dynamique des feux.
- En Sibérie, au Sud-Est de la Russie, la région du lac Baïkal, où le climat très continental est plus rude que dans les deux autres régions.

La question de l'histoire des feux est traitée par le chapitre II (augmentation progressive de l'activité des feux de forêt pendant l'Holocène dans la région du Nord de l'Oural (République de Komi, Russie) et par le chapitre V (Synthèse sur les relations entre le feu, la végétation et le

climat au cours de l'Holocène en République de Komi et comparaison de l'activité des feux de la Carélie, la République de Komi et la région du Lac Baïkal). L'hypothèse établie pour le chapitre II est que la fréquence des feux en République de Komi risque d'être plus importante à la fin de l'Holocène, lorsque la population humaine augmente dans cette région, et que son influence sur le feu devient plus importante. La synthèse sur les relations feu-végétation-climat permet de tester l'hypothèse selon laquelle l'activité de feu sera moins forte sous un climat humide et froid, associé à une taïga sombre, mais plus forte avec un climat chaud et sec, associé à une taïga claire (Goldammer and Furyaev, 1996; Schulze et al., 2005; Ali et al., 2012). La comparaison du régime des feux des trois zones d'étude permettra de tester l'hypothèse selon laquelle les différents climats qui correspondent à chaque région auront des impacts différents sur les régimes des feux des zones correspondantes.

Cette thèse traite de manière plus approfondie les relations feux-végétation de l'Holocène en République de Komi, qui seront présentés en chapitre III (Dynamique de végétation en République de Komi au cours de l'Holocène). Ce chapitre repose sur l'hypothèse que la fréquence des feux établie en République de Komi au cours de l'Holocène (par le biais du chapitre II) est associée à un type de taïga définie : lorsque la fréquence des feux sera faible, l'on s'attend à trouver une végétation de type taïga sombre, alors que lorsque la fréquence des feux est élevée, l'on s'attend à trouver une forêt de type taïga claire. Le chapitre IV est dévolu à l'étude du climat de l'Holocène en République de Komi à partir de l'étude conjointe des données polliniques et des brGDGTs (Interactions entre le climat, la végétation et les incendies dans l'Oural du Nord (République de Komi, Russie) pendant l'Holocène : une approche multi-proxy). L'hypothèse testée dans ce chapitre est que le climat reconstruit (températures et précipitations) sera en adéquation avec l'activité de feu et la dynamique de végétation enregistrée, c'est-à-dire les périodes chaudes et sèches associées à une activité de feu élevée et à la mise en place d'une taïga claire. De plus, l'utilisation de ces deux types de proxy doit nous permettre de mieux distinguer les variations majeures du climat dans la zone d'étude, même s'ils ne répondent pas aux mêmes forçages.

1. 3. LES ZONE D'ETUDE ET STRATEGIES D'ECHANTILLONNAGE

L'objectif de cette thèse est de déterminer quelle a été la dynamique des incendies, de la végétation et du climat de l'Holocène et leurs interactions dans ces trois régions de Russie :

la République de Komi, la Carélie et la région du Lac Baïkal (Figure I.4). Elle a débuté par une campagne de terrain en République de Komi, en Septembre 2016 (Figure I.5). Les analyses concernant l'activité de feux se sont déroulées de Janvier à Juin 2016. Celles concernant la dynamique de végétation, de Janvier à Août 2017 et celles concernant le climat de l'Holocène, de Septembre 2018 à Mai 2019. En Mars 2017, la campagne de terrain en Carélie a été réalisée et l'analyse de l'activité des feux passés s'est déroulée d'Avril 2017 à Juin 2017 (Figure I.5). La campagne de terrain de la région Lac Baïkal a eu lieu en Juillet 2017, et a été l'objet des travaux de deux stagiaires M2, pour l'étude de l'activité de feux passés, dans le cadre du financement Equipe de Recherche Junior, du Labex Cemeb, de Janvier à Juillet 2019 (Figure I.5).

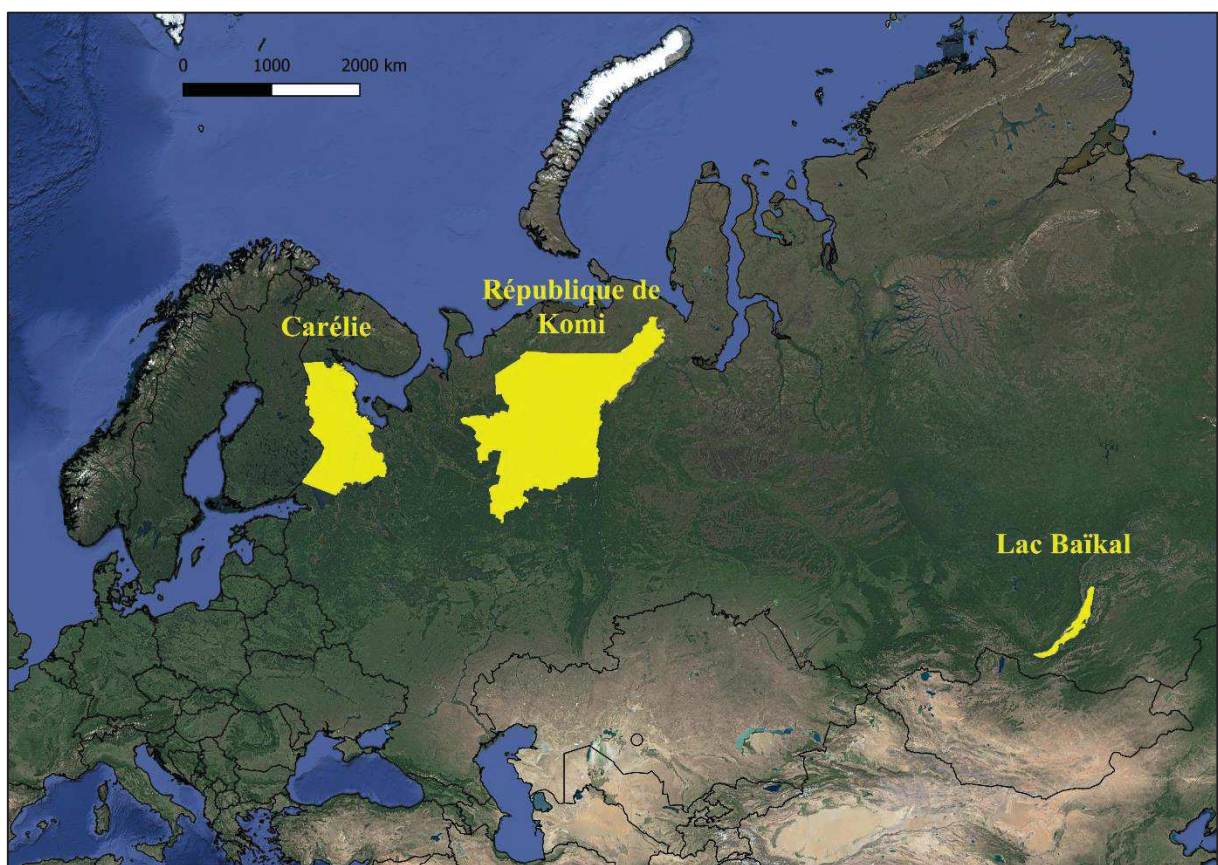


Figure I.4 : Carte des trois zones d'études en Russie : la Carélie, la République de Komi et la région du Lac Baïkal

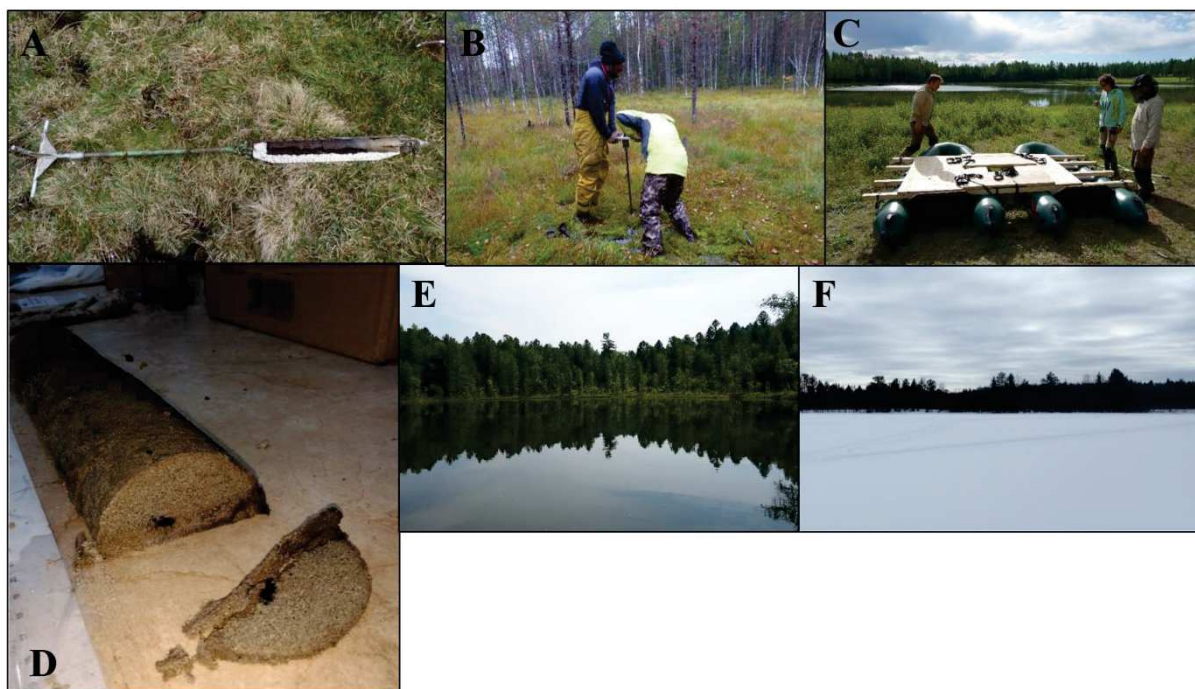


Figure I.5 : A. Carottier russe. B. Carottage d'une des tourbières forestières à Yaksha. C. Plateforme utilisée pour le terrain dans la région du Lac Baïkal. D. Découpe d'une carotte sédimentaire issue de la République de Komi, au laboratoire. E. Lac Jarod. F. Lac Vohto1.

L'étude de la végétation passée est en général réalisée à l'aide de l'étude des grains de pollen conservés dans les carottes sédimentaires (lacs et tourbières). Ces analyses palynologiques permettent de représenter la présence des espèces productrices de grains de pollens transportés essentiellement par le vent. Cependant des biais peuvent apparaître, car la production de pollen n'est pas la même d'une espèce à l'autre. Certaines espèces produisent beaucoup de pollen, comme par exemple les pins, alors que d'autres en produisent beaucoup moins, comme par exemple le sapin. Pour prendre en compte ces différents biais et retracer au mieux la végétation à partir des grains de pollen, des algorithmes et des modèles ont été développés au cours de la dernière décennie. Parmi ces derniers, le modèle REVEALS (Regional Estimates of Vegetation Abundance from Large Sites), a ainsi pour objectif d'estimer le couvert de végétation régional, de 10^6 à 10^7 ha (et non plus seulement les pourcentages polliniques), à partir de l'information recueillie par les comptages polliniques de plusieurs sites d'études (Sugita, 2007a; Sugita et al., 2010; Hultberg et al., 2015). Cette approche a été développée, testée et validée par l'étude de différents sites de la forêt boréale de Suède, mais également pour d'autres types d'écosystèmes, comme ceux du plateau tibétain, pour l'Holocène

(Anderson et al., 2006; Broström et al., 2008; Hellman et al., 2008; Sugita et al., 2010; Wang and Herzschuh, 2011).

Pour retracer les variations des climats passés, différents bioindicateurs ou proxies peuvent être utilisés : pollen, chironomes, coléoptères, spéléothèmes etc. (e.g. Bini et al., 2018). Ainsi les chironomes et les coléoptères permettent de quantifier la température du mois le plus chaud alors que les grains de pollen et les spéléothèmes permettent également de documenter les précipitations. Chaque proxy possède ses points forts et ses faiblesses, il est donc important de les coupler au sein d'études multi-proxies (Peyron et al., 2013). Il peut ainsi s'avérer délicat de discuter de la dynamique de la végétation si cette dernière est quantifiée à partir des mêmes données polliniques. Dans ce cas, d'autres proxies peuvent être utilisés comme paléothermomètre : récemment des biomarqueurs moléculaires appelés branched Glycerol Dialkyl Glycerol Tetraethers (brGDGTs) ont été identifiés. Ce sont des molécules membranaires de lipides d'origine bactérienne et ubiquistes des sols, tourbières, lacs, rivières et océans (Damsté et al., 2000; Weijers et al., 2006). Leur distribution est liée à la température et au pH de leur milieu (Weijers et al., 2007a; Peterse et al., 2010). De tels marqueurs peuvent se révéler utiles pour étudier les relations végétation-température de manière indépendante.

1.3.1. La République de Komi

La République de Komi (Figure I.6A) constitue la région d'étude majeure de la thèse puisqu'elle fait l'objet de l'analyse conjointe des feux, de la végétation et du climat. La République de Komi est une région administrative de Russie (415900 km²), qui se trouve entre les latitudes 59°12'N et 68°25'N et entre les longitudes 45°25'E et 66°10'E. La température annuelle moyenne varie de -6°C au Nord, à +1°C au Sud. Les précipitations annuelles sont comprises entre 450 et 700 mm (Zaboeva, 1997; Drobyshev et al., 2004a). Le relief est principalement plat, excepté la partie Est de la région située sur les contreforts de l'Oural (Naryshkin, 2003). La forêt boréale de cette région est composée de *Picea* spp., *Pinus sylvestris* et *Betula* spp., répartis en mosaïque de taïga sombre et de taïga claire (Naryshkin, 2003; Golubeva, 2008). La République de Komi est soumise aux influences climatiques provenant de la côte atlantique à l'Ouest, mais aussi des systèmes de blocages (hautes pressions atmosphériques) provenant de la Sibérie (Goldammer and Furyaev, 1996; Drobyshev et al., 2004a). Dans le sud de la République de Komi, trois tourbières ont été échantillonnées à Yaksha

(Yak1, Yak2 et Yak3, noms non-officiels, Figure I.6B, altitude moyenne 135 m *a.s.l.*). Les études de dendrochronologie, sur les arbres présentant des cicatrices de feux, ont été réalisées pour les sites Yak1, Yak2 et Yak3. Les carottes sédimentaires ont été prélevées sur les sites Yak2 et Yak3, au centre (Yak2-A et Yak3-B) et en périphérie (Yak2-B et Yak3-B). Une approche multi-proxie a été effectuée sur les carottes Yak2-A et Yak3-A, combinant l'analyse des charbons, des grains de pollen et des biomarqueurs moléculaires (brGDGTs).

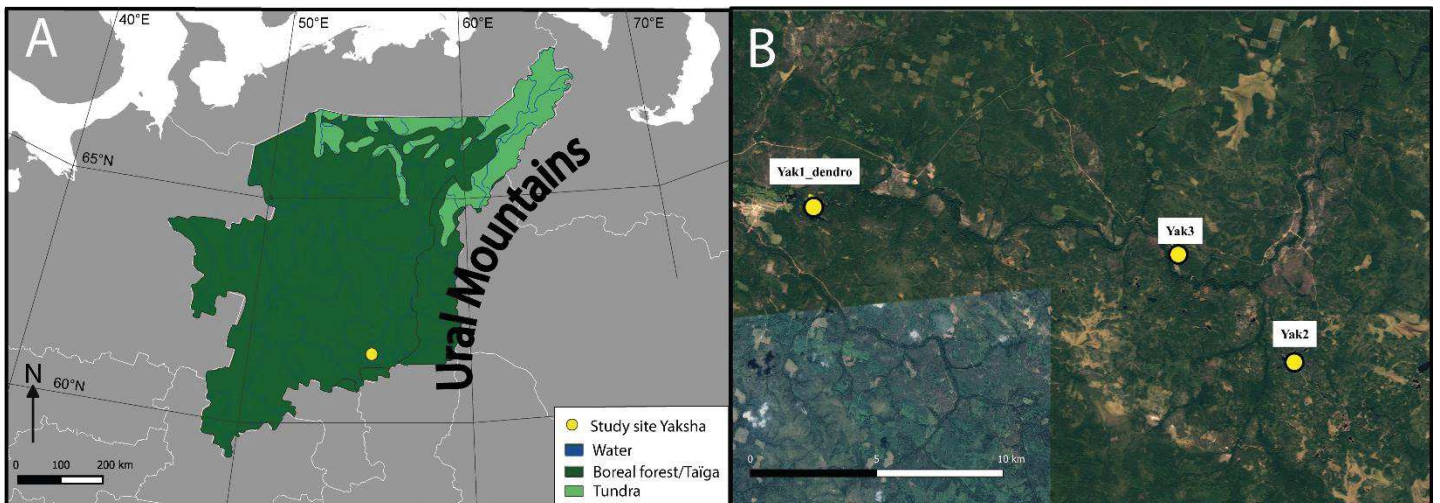


Figure I.6 : A. République de Komi en Russie. B. Les trois tourbières étudiées en République de Komi

1.3.2. La Carélie

La région de la Carélie (Figure I.7) a été étudiée à travers l'analyse des sédiments lacustres de deux lacs (Vohto 1, 62°12'24.70"N 33°34'38.39"E et Vohto 2, 62°12'37.44"N 33°35'54.82"E, noms non-officiels, altitude 180 m *a.s.l.*), proches du lac Onega et de la ville Petrozavodsk (capitale de la Carélie). Le diamètre du lac Vohto1 est de 320 m et celui de Vohto2, de 445 m. Le climat est un climat de transition entre un climat de type océanique et un climat de type continental (Filatov and Rukhovets, 2012). En moyenne, les précipitations sont de l'ordre de 550 à 750 mm par an et les températures annuelles moyennes sont de l'ordre de 1.5°C (Filatov and Rukhovets, 2012). Dans cette région, la topographie a été modulée par la longue présence des glaciers passés et est ondulante (Kuusmanen et al., 2014). La végétation actuelle est composée principalement de *Picea abies* et de *Pinus sylvestris* et donc un mélange

de taïga sombre et taïga claire (Kuusmanen et al., 2014). Les deux lacs ont été analysés en termes de charbons, *via* l'étude des deux carottes sédimentaires.

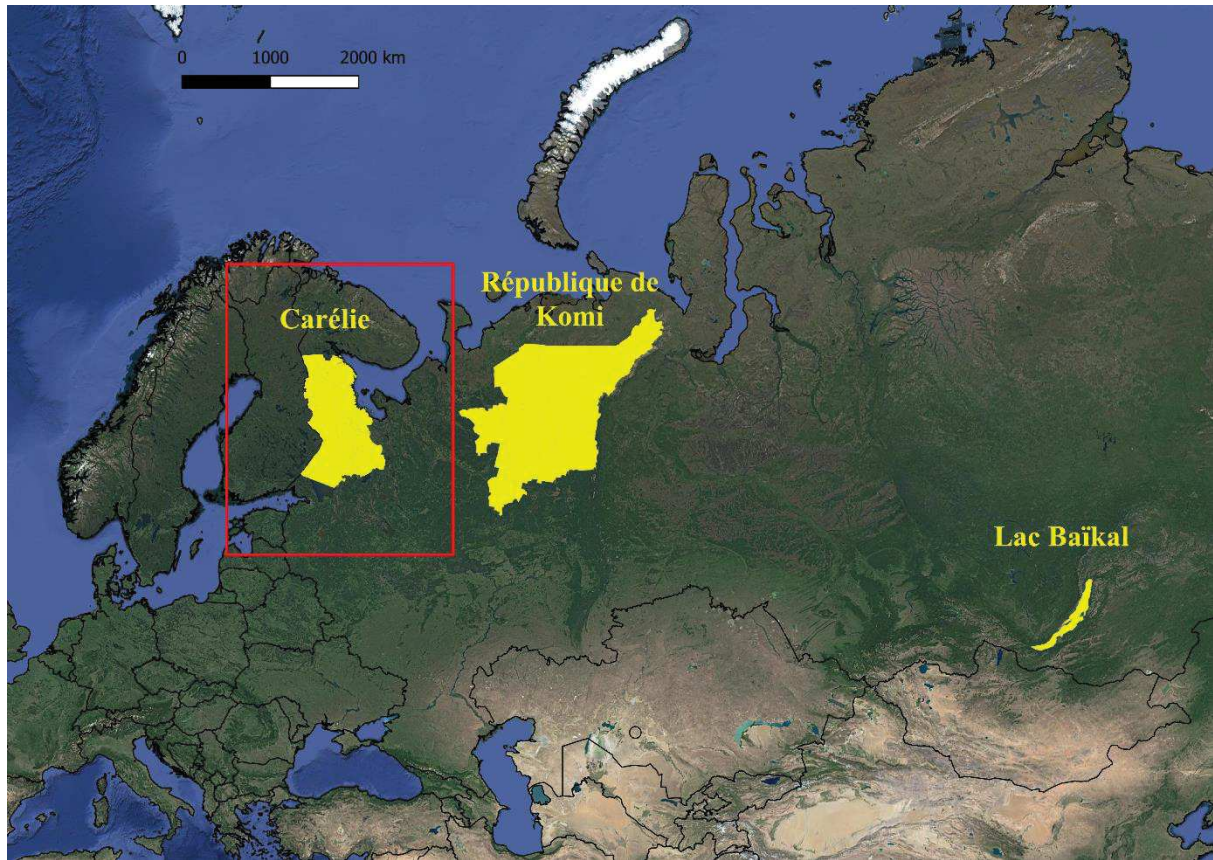


Figure I.7 : Mise en avant de la Carélie par rapport aux autres régions d'étude

1.3.3. La région du Lac Baïkal

La région du Lac Baïkal (Figure I.8) étudiée ici est située au sud de celui-ci. Des analyses de charbons de bois ont été effectuées à partir de carottes prélevées dans deux sites lacustres, le lac Ebène (51°28'57.65"N, 104°50'12.21"E, altitude : 496 m *a.s.l.*, profondeur = 110 cm, diamètre = 80 m), et le lac Jarod (51°26'50.62"N, 104°50'55.07"E, altitude 453 m *a.s.l.*, profondeur = 635 cm, diamètre = 180 m) (noms non-officiel). Le climat dans cette région est de type continental et montre une amplitude des températures qui va de -18.7°C en janvier à +15.4°C en juillet (Bezrukova et al., 2013). Les précipitations annuelles sont comprises entre 800 et 900 mm (Bezrukova et al., 2013). La forêt qui entoure les deux sites d'étude est de la taïga sombre, composée principalement de *Pinus sibirica*, *Betula* spp., *Picea obovata*, *Abies*

sibirica et d'individus de *Pinus sylvestris*. Les deux lacs ont été analysés en termes de charbons, via l'étude des carottes sédimentaires.

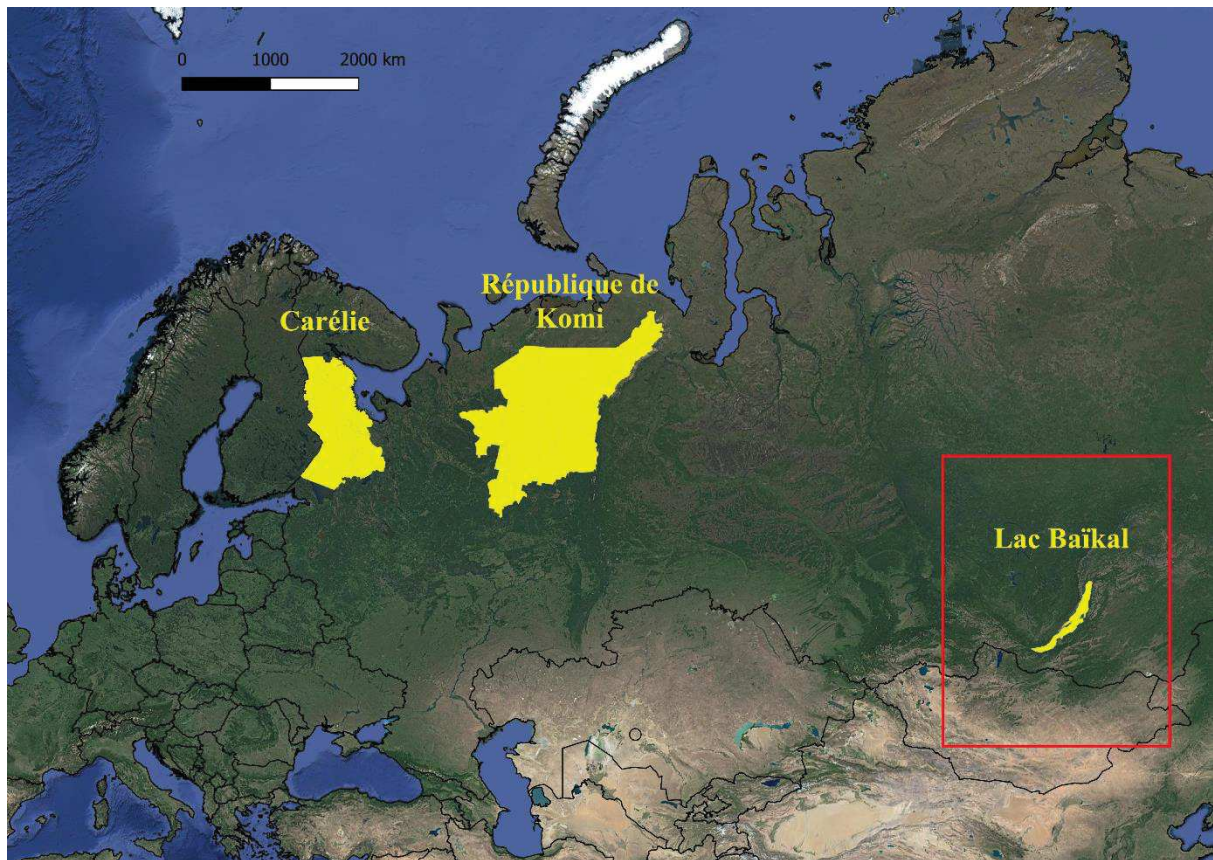


Figure I.8 : Mise en avant du Lac Baïkal par rapport aux autres régions d'étude

1. 4. LA PALEOECOLOGIE : DES OUTILS ET METHODES POUR RECONSTITUER LES CHANGEMENTS ENVIRONNEMENTAUX

I.4.1. Analyse des charbons de bois et des cicatrices de feux des arbres

Pour analyser et déterminer l'histoire des feux au cours de l'Holocène, deux méthodes complémentaires ont été utilisées : l'analyse des charbons de bois séquestrés dans les carottes sédimentaires afin d'avoir accès à l'ensemble de l'histoire des feux de l'Holocène ; et pour des périodes récentes, l'analyse des cicatrices laissées par des feux sur les troncs des arbres permet d'accéder de manière très précise aux évènements de feux qui ont eu lieu plus récemment (durant les 700 dernières années).

Chaque carotte sédimentaire étudiée est accompagnée par un modèle d'âge, lui-même basé sur les datations d'échantillons le long de la carotte sédimentaire (entre 5 à 7 datations par carotte, analyses réalisées par le laboratoire Beta Analytic Testing Laboratory et le laboratoire de Radiochronologie de l'Université de Laval). Les modèles d'âge ont été réalisés avec le package R CLAM 2.2 pour la République de Komi (Blaauw, 2010) et le package WinBacon pour la Carélie et la région du Lac Baïkal (Blaauw and Christen, 2011).

Au laboratoire, chaque carotte sédimentaire étudiée a été divisée en sous-échantillons de 0.5 cm d'épaisseur. Un sous-échantillon de 1cm³ a ensuite été extrait (au cœur de la tranche de 0.5 cm d'épaisseur), puis trempé dans une solution de 25 mL de Javel, 3g. de NaPO₃ et 0.5g de KOH, sur un agitateur pendant une période minimale de 24h (Carcaillet et al., 2001). Le substrat était alors filtré à travers un tamis d'une épaisseur de 160 µm, afin de sélectionner les charbons les plus représentatifs des feux locaux (Higuera et al., 2007a; Ali et al., 2009a; van Bellen et al., 2012). Les particules de charbons ainsi extraites ont été comptées et mesurées à l'aide du logiciel WinSeedle (WinSEEDLE™software; Regent Instruments Inc., <http://regent.qc.ca/>). La surface des charbons a été utilisée comme indice pour calculer la fréquence des feux (Ali et al., 2009b). Le logiciel CharAnalysis a ensuite été utilisé pour mettre en évidence la fréquence des feux à partir de pics significatifs et calculer le retour d'intervalle des feux (Fire Return Interval, FRI, soit le nombre d'années entre deux incendies consécutifs à un endroit donné) (Higuera et al., 2007a). Les mesures de charbons CHAR ont été interpolées à l'aide de la médiane de la résolution de chaque échantillon (Higuera et al., 2011). Les séries CHAR ont été divisées entre les séries de basses fréquences (le bruit de fond) et les séries de hautes fréquences (les pics de charbons). Les séries correspondantes aux pics de charbon de bois représentent l'information relative aux dates des incendies qui ont lieu dans les zones d'études, au cours de l'Holocène. Ces dates nous ont permis d'établir la fréquence et le FRI. Pour la République de Komi, une fonction de densité Kernel a été utilisée pour interpoler les résultats des sites et ainsi obtenir un signal régional de l'activité de feu (Mudelsee et al., 2004).

L'analyse des cicatrices de feux des cernes a été réalisée seulement pour les sites de République de Komi. Autour de chaque site (dans un rayon de 200 m), les pins sylvestres présentant des cicatrices de feux (Figure I.9A) ont été sélectionnés et ont fait l'objet d'une section transversale afin de dater par comptage des cernes, les événements de feux, visibles grâce aux cicatrices laissés (Arno and Sneck, 1977; Brossier et al., 2014). Les sections (Figure I.9B) ont été séchées puis polies en laboratoire pour visualiser les cernes et localiser précisément les cicatrices de feux (Schweingruber, 2012; Brossier et al., 2014). Un microscope binoculaire (Leica M80) a permis l'identification et la datation des cicatrices selon les méthodes de dendrochronologie standards (Stokes and Smiley, 1968; Niklasson et al., 2010).

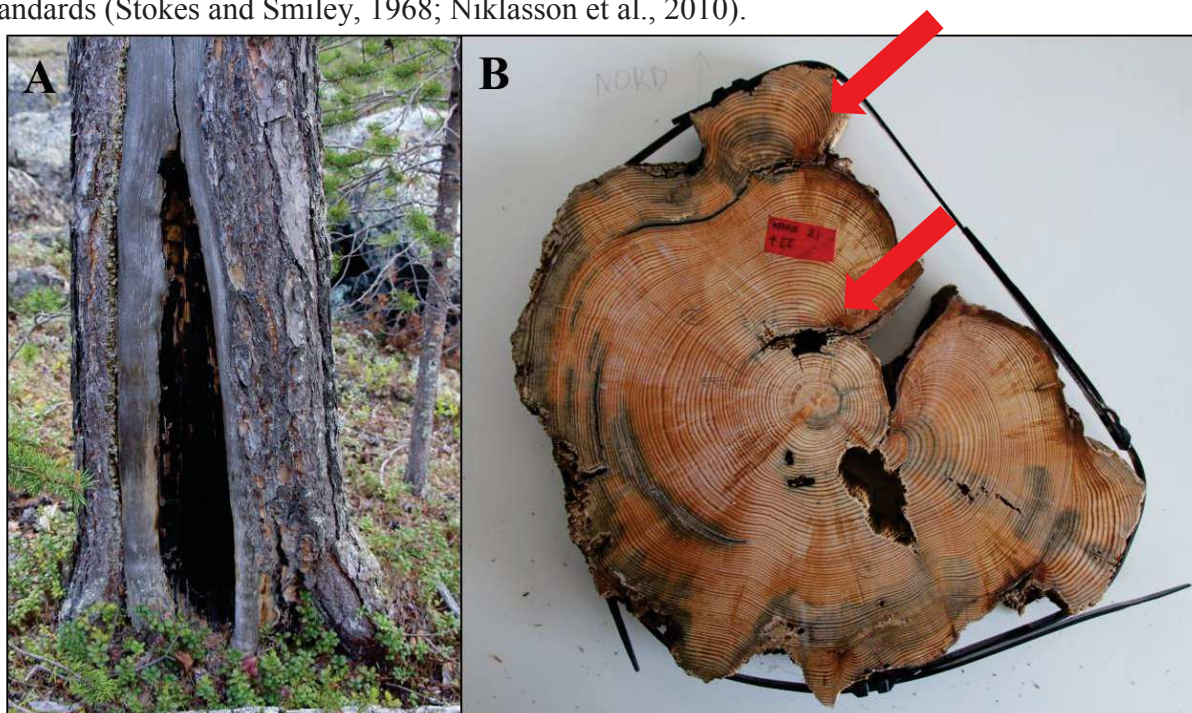


Figure I.9 : A. *Pinus sylvestris* présentant une cicatrice de feu. B. Section d'un tronc de *Pinus sylvestris* présentant des cicatrices de feu au niveau de certains de ces cernes. Photos G. Magne (ISEM)

1.4.2. Analyse palynologique et algorithme de reconstitution de la végétation

La dynamique de la végétation au cours de l'Holocène en République de Komi a été étudiée à partir de l'analyse des grains de pollen des carottes des sites Yak2-A et Yak3-A, et de l'application du modèle REVEALS à plusieurs séquences polliniques de la région.

Afin de comparer les signaux de pollen et de charbon de bois, et donc de couvrir le maximum de temps, une séquence composite a été construite à partir des carottes Yak3-A et Yak2-A.

L'intervalle de 0 à 300 cm de la carotte Yak3-A offrait la meilleure résolution temporelle de l'Holocène et son sommet a été conservé (contrairement à Yak2-A). Les échantillons ont été prélevés tous les 6 à 10 cm. La partie inférieure de la carotte Yak2-A a aussi permis d'accéder au début de l'Holocène, mais avec une résolution temporelle inférieure à celle de Yak3-A. Les échantillons y ont été prélevés tous les 3 cm. Des échantillons de contrôle ont été prélevés tous les 25 cm pour les 100 premiers cm (chevauchement avec la carotte Yak2-A). Un sous-échantillon de sédiments de 3 cm³ provenant du centre de chaque tranche de 0.5 cm d'épaisseur a subi un traitement chimique (HCl, KOH, HF, acétolyse) et un double tamisage pour garder la fraction entre 200 et 10 µm (protocole adapté de Moore et al., 1991). L'analyse des grains de pollen a été réalisée avec un microscope optique à un grossissement standard de 400x. Trente-neuf types de pollen ont été identifiés à l'aide de la collection de référence de l'ISEM et des atlas photos (Reille, 1992; Beug, 2004). Les deux espèces de *Pinus* (*sibirica* et *sylvestris*, Figure I.10) ont été identifiées tandis que les sous-espèces *Betula* spp. (*pendula* et *pubescens*) et *Picea* (*abies* et *obovata*) n'ont pas été distinguées. Un minimum de 300 grains de pollen a été compté par échantillon.

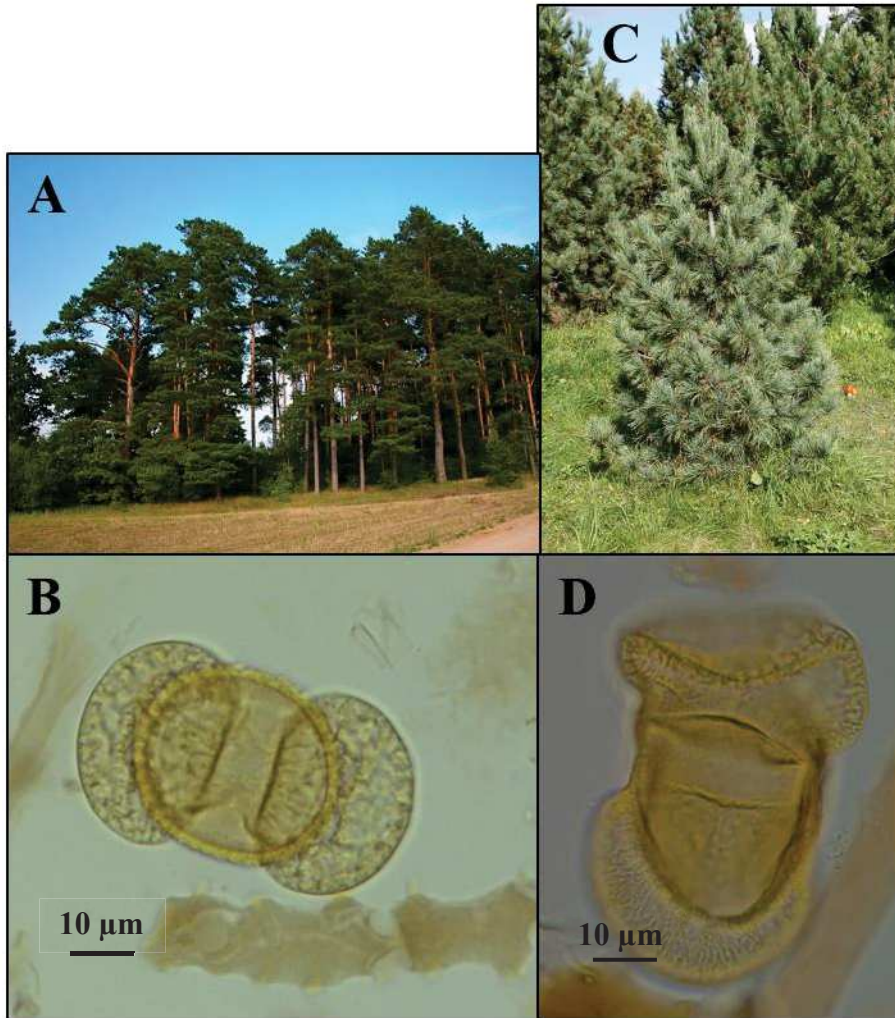


Figure I.10 : A. Forêt de *Pinus sylvestris*. B. Pollen de *Pinus sylvestris*. C. Individu de *Pinus sibirica*. D. Pollen de *Pinus sibirica*

Pour corriger le signal pollinique et quantifier au mieux les couvertures végétales régionales dans la zone d'étude, le modèle REVEALS a été utilisé (Sugita, 2007a). Les paramètres requis pour le modèle REVEALS sont le rayon du bassin versant, les estimations de la productivité du pollen et le taux de chute des grains de pollen par espèce. Ces paramètres sont souvent dépendant de la région étudiée, en particulier les valeurs de PPE (Pollen Productivity Estimation, soit l'estimation de la productivité pollinique). Les valeurs de PPE n'étant pas disponibles pour la région de la République de Komi et nous avons choisi d'utiliser les valeurs de l'étude menée la plus proche et la plus semblable en terme de climat et de composition forestière (en Estonie ; Poska et al., 2011). Le modèle REVEALS permet de corriger le signal régional des sites d'enregistrement de grandes tailles (Sugita, 2007a) et, par conséquent, le

signal de végétation de Yaksha a été comparé à d'autres signaux dans un rayon de 500 km du site (distance justifiée dans Cao et al., 2018). Cinq séquences polliniques analysées dans des études précédentes ont été utilisées ici selon un transect du sud vers le nord, avec la conception d'un nouveau modèle d'âge lorsque cela était nécessaire (Sidorchuk et al., 2001; Golubeva, 2008). Les calculs ont été effectués avec le logiciel REVEALS 5.0 et le modèle de Prentice (Prentice, 1985) qui combine la vitesse du vent (de $3\text{m}\cdot\text{s}^{-1}$), et le rayon de chaque lac ou tourbière étudié.

1.4.3. Pollen, biomarqueurs moléculaires et quantification des paramètres climatiques

La quantification des températures et des précipitations passées a été réalisée uniquement pour la République de Komi, à l'aide de deux marqueurs biotiques indépendants : les données polliniques (Guiot, 1990; Peyron et al., 2013) et les brGDGTs (Damsté et al., 2000; Weijers et al., 2006). Ces derniers sont des biomarqueurs d'origine bactérienne (lipides membranaires) et ont l'avantage d'être un paléothermomètre direct (calibration) alors qu'il faut passer par une fonction de transfert pour quantifier les températures à partir des données polliniques.

Afin de quantifier avec le plus de fiabilité possible les paléoclimats à partir des données polliniques, nous avons choisi de privilégier une approche de type multi-méthode. La reconstruction quantitative des températures annuelles moyennes, des précipitations annuelles, des températures du mois le plus chaud et le plus froid a été réalisée avec deux méthodes différentes : la technique des analogues modernes ou meilleurs analogues « MAT » (Guiot, 1990) et la WAPLS, Weighted averaging partial least squares regression (ter Braak and Juggins, 1993). La MAT est une méthode basée sur la comparaison d'assemblages polliniques alors que la WAPLS est une fonction de transfert. La MAT vise à comparer les assemblages polliniques modernes (dont les paramètres climatiques sont connus) avec les assemblages polliniques fossiles, par le calcul d'une distance (distance de Chord). Si les assemblages polliniques actuels et fossiles sont trop différents (seuil défini par une méthode de Monte-Carlo), les assemblages modernes ne sont pas pris en compte. Au contraire, les assemblages modernes qui sont les plus proches des fossiles sont sélectionnés en tant que « meilleurs analogues » et leurs variables climatiques sont moyennées (après pondération par la distance). La WAPLS est une méthode de régression qui suppose que le climat et les assemblages de pollen sont liés par une relation

unimodale. Chaque espèce est liée à un optimum climatique mais ne peut pas se développer lorsque certains paramètres climatiques atteignent des valeurs critiques pour l'espèce. Ces deux méthodes sont basées sur un référentiel de 2115 données polliniques actuelles (sols, mousses et sommets de carottes sédimentaires) localisées en Eurasie. Le climat au site Yaksha et à l'échelle régionale du sud de la République de Komi a ainsi pu être quantifié.

La seconde méthode utilisée pour reconstruire les températures passées au site Yaksha utilise les biomarqueurs moléculaires brGDGTs. Pour effectuer l'analyse des brGDGTs, 26 échantillons provenant de Yak3-A et 12 échantillons de Yak2-A ont été étudiés à l'ENS de Lyon (LGLTPE, France). Les échantillons ont été lyophilisés et réduits en poudre. Dans des aliquotes de moins d'un gramme, on a ajouté une solution étalon de C46, à $10 \text{ ng} \cdot \mu\text{L}^{-1}$ (Huguet et al., 2006). Ensuite, les lipides ont été placés dans une micro-onde (MARS, CEM), avec du dichlorométhane (DCM):MeOH (3:1). Les extraits lipidiques totaux ont été séparés en fraction polaire et apolaire sur une colonne d'alumine Al_2O_3 (1 g) avec de l'hexane:DCM (1:1) et DCM/MeOH (1:1). Les fractions ont ensuite été analysées grâce à un spectromètre de masse à chromatographie liquide à haute performance (HPLC-MS, Agilent 1200, Hopmans et al., 2016; Davtian et al., 2018).

Les masses obtenues ont servi à calculer des indices indicateurs des températures du milieu (Tableau IV.2). Trois calibrations de températures moyenne de l'air ont été utilisées pour estimer les températures de la zone d'étude, au cours de l'Holocène : la température annuelle moyenne $\text{MAT}_{\text{Peterse}}$, calibrée à l'aide d'un jeu de donnée global, d'après Peterse et al. (2012), la température d'été moyenne MSAT , calibrée avec des lacs situés en Antarctique, d'après Foster et al. (2016) et la température annuelle moyenne $\text{MAAT}_{\text{peat}}$, calibrée avec des tourbières du monde entier, d'après Naafs et al. (2017).

Chapitre II.

AUGMENTATION PROGRESSIVE DE L'ACTIVITE DES FEUX DE FORET PENDANT L'HOLOCENE DANS LA REGION DU NORD DE L'OURAL (REPUBLIQUE DE KOMI, RUSSIE)

Gradually increasing forest fire activity during the Holocene in the northern Ural region (Komi Republic, Russia)

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Research Paper

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Abstract

In many boreal regions of Russia the past natural variability of forest fire activity remains largely undocumented, preventing accurate assessment of the impact of current climate warming on forest ecosystem dynamics. This study aims to reconstruct the Holocene fire history of the northern Ural mountain foothills, in the Komi Republic, based on analyses of charcoal particles from peatland deposits and coupled with dendrochronological investigations. The results show that there was a gradual increase in forest fire activity during the past 11,000 years. Between 11,000 and 5100 cal. yr BP, the mean fire return interval (FRI) oscillated between 600 and 200 years. During this period, regional data showed that cold temperature, humid climatic conditions, combined with steppe vegetation between 11,000–9000 cal. BP, and then the development of spruce-dominated forest between 9300 and 4600 cal. yr BP, were less conducive to fires. After 5100 cal. yr BP, a gradual increase in drought conditions through reduced precipitations, associated with the establishment of a Scots pine forest favored fire frequency, with a mean FRI under 200 years (range, 200–40 years). Nowadays (since CE 1500), human activity induces an unprecedented fire activity with a mean FRI below 100 years (range, 100–40 years).

Keywords

boreal forest, charcoal particles, dendrochronology, peatland, tree rings, wildfires

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2.1. ABSTRACT

In many boreal regions of Russia the past natural variability of forest fire activity remains largely undocumented, preventing accurate assessment of the impact of current climate warming on forest ecosystem dynamics. This study aims to reconstruct the Holocene fire history of the northern Ural mountain foothills, in the Komi Republic, based on analyses of charcoal particles from peatland deposits and coupled with dendrochronological investigations. The results shows that there was a gradual increase in forest fire activity during the last 11 000 years. Between 11000 and 5100 cal. yr BP, the mean Fire Return Interval (FRI) oscillated between 600 to 200 years. During this period, regional data showed that cold temperature, humid climatic conditions, combined with steppe vegetation between 11000-9000 cal. BP, and then the development of spruce-dominated forest between 9300-4600 cal. yr BP, were less conducive to fires. After 5100 cal. yr BP, a gradual increase in drought conditions through reduced precipitations, associated with the establishment of a Scots pine forest favored fire frequency, with a mean FRI under 200 years (range 200 to 40 years). Nowadays (since CE 1500), human activity induces an unprecedented fire activity with a mean FRI below to 100 years (range 100 to 40 years).

Keywords: Boreal Forest ; Peatland ; Charcoal particles ; Dendrochronology ; Tree-rings ; Wildfires

2.2. INTRODUCTION

The northern boreal forest represents almost 30% of the world's forested areas and contains the largest reservoir of terrestrial carbon stored in soil and peatlands (Gorham, 1991; Sheng et al., 2004). Boreal forest dynamics have an impact on the carbon composition of the atmosphere and global climate dynamics (Foley et al., 1994; Kasischke and Stocks, 2012).

Fire is the main natural disturbance in this biome, impacting the diversity, composition and structure of the forest. Projected climate warming may therefore increase fire activity through extension of the fire season and drought severity (Flannigan et al., 2009; Bergeron et al., 2011). Current global warming may also increase net biomass production (Flannigan et al., 2009) and forest fuel, creating more favorable conditions for fire activity (Gauthier and Vaillancourt, 2008; Flannigan et al., 2009). In the boreal zone, fire is an important environmental and socio-economic issue for governments (Conard and Ivanova, 1997; Weber and Flannigan, 1997; Stocks et al., 1998; Randerson et al., 2006; Soja et al., 2007; Stocker, 2014). For example, in Canada, fire suppression policy expenditure and costs have been increasing since the 1970s (Stocks and Martell, 2016) and, based on current projections, will continue to increase.

The impacts of fire on boreal forest vegetation depend on different variables that define the fire regime, *i e* its frequency, severity and intensity. (Keeley, 2009). In North American boreal forests, wildfires are generally crown fires (Kasischke and Stocks, 2012; de Groot et al., 2013; Stocks and Martell, 2016), destroying stand canopy and leading to a total renewal of pre-fire cohorts. In contrast, in the Eurasian boreal forest, a mixed severity fire regime dominates, with a considerable proportion being surface fires (Goldammer and Furyaev, 1996). Across this ecozone, NOAA-AVHRR satellite data have shown an increase in burned areas, with an annual average of 9.3 million hectares for the period 1996–2005 (Goldammer, 2015), and the number of fires has varied between 10000 and 30000 per year (Gauthier and Vaillancourt, 2008).

To better understand the mechanisms that link climate, vegetation and fire, particularly under the yoke of climate change, it is important to characterize the natural range of variability of fire events over time. For this, paleoecological investigations are needed to provide a better understanding of fire activity and interactions with both climatic oscillations and human activity (Randerson et al., 2006; Whitlock et al., 2010; Clear et al., 2014). According to our knowledge such data is not available for the northern Ural Mountains foothills, preventing the accurate assessment of the impact of current climate change on fire frequency.

Here we reconstruct Holocene fire frequency for the north-western foothills of the Ural Mountains, in the Komi Republic based on charcoal particles sequestered in two peatlands coupled with dendrochronological investigations. Our goal is to give an overview of the fire frequency changes during the Holocene in the study zone, and then to indicate the first lines of thought to understand the mechanisms underlying fire activity, which is intrinsically linked to the dynamic of vegetation, climate and human activities. We hypothesized that periods with dry climatic conditions (either with warm or cold temperatures) would be more conducive to fires compared with cold and/or wet periods (either with warm or cold temperatures). For example, in Québec, in Alaska and in Scandinavian boreal forests (Higuera et al., 2009; Ali et al., 2012; Girardin et al., 2013; Blarquez et al., 2015; Drobyshev et al., 2015), results showed a warm and dry period favorable for fires before 4000 cal. (calibrated) yr (years) BP (before present), followed by colder and wetter conditions less favorable to fire activity. The same pattern has been recorded in Fennoscandia (Clear et al., 2014; Drobyshev et al., 2016). In the study zone, we suspect greater fire activity at the end of the Holocene, when the human population increased and its impact on forest fires became more significant (Naryshkin et al., 1999; Drobyshev et al. 2004).

2.3 METHODS

2.2.1. The study area

The Komi Republic (415 900 km²) is situated between 59°12' and 68°25'N and between 45°25' and 66°10'E (Figure II.1). The mean annual temperature varies between -6°C and +1°C from south to north, and the annual precipitation varies between 450 and 700 mm (Drobyshev et al., 2004a). Moraine and surface loams (Zaboeva, 1997; Drobyshev et al., 2004a) with podzolic soils (Naryshkin, 2003) dominate in the region. There is discontinuous permafrost (Christensen and Kuhry, 2000). The majority of the relief is flat, except near the Ural Mountains (Naryshkin, 2003). Light taiga forests are observed in the Komi Republic, mainly composed of Scots pine (*Pinus sylvestris*), birch (*Betula pendula* and *Betula pubescens*) and spruce (*Picea abies* s.l.).

The Komi Republic was only sparsely inhabited during the Holocene until about 1500 CE (Common Era). Before this time there was likely no human activity in this area. After that, human population density increased significantly from 20000 inhabitants in the 16th century to

more than 1.12 million inhabitants at the beginning of the 21st century (Drobyshev et al., 2004a; Klein Goldewijk et al., 2011). The population density is less than two per square kilometer, and for the study area, it is less than one person per square kilometer. The nearest settlements to the sampling points are Timsher and Lopyuvad, which were created in 1932 (<http://timsher.selakomi.ru/>).

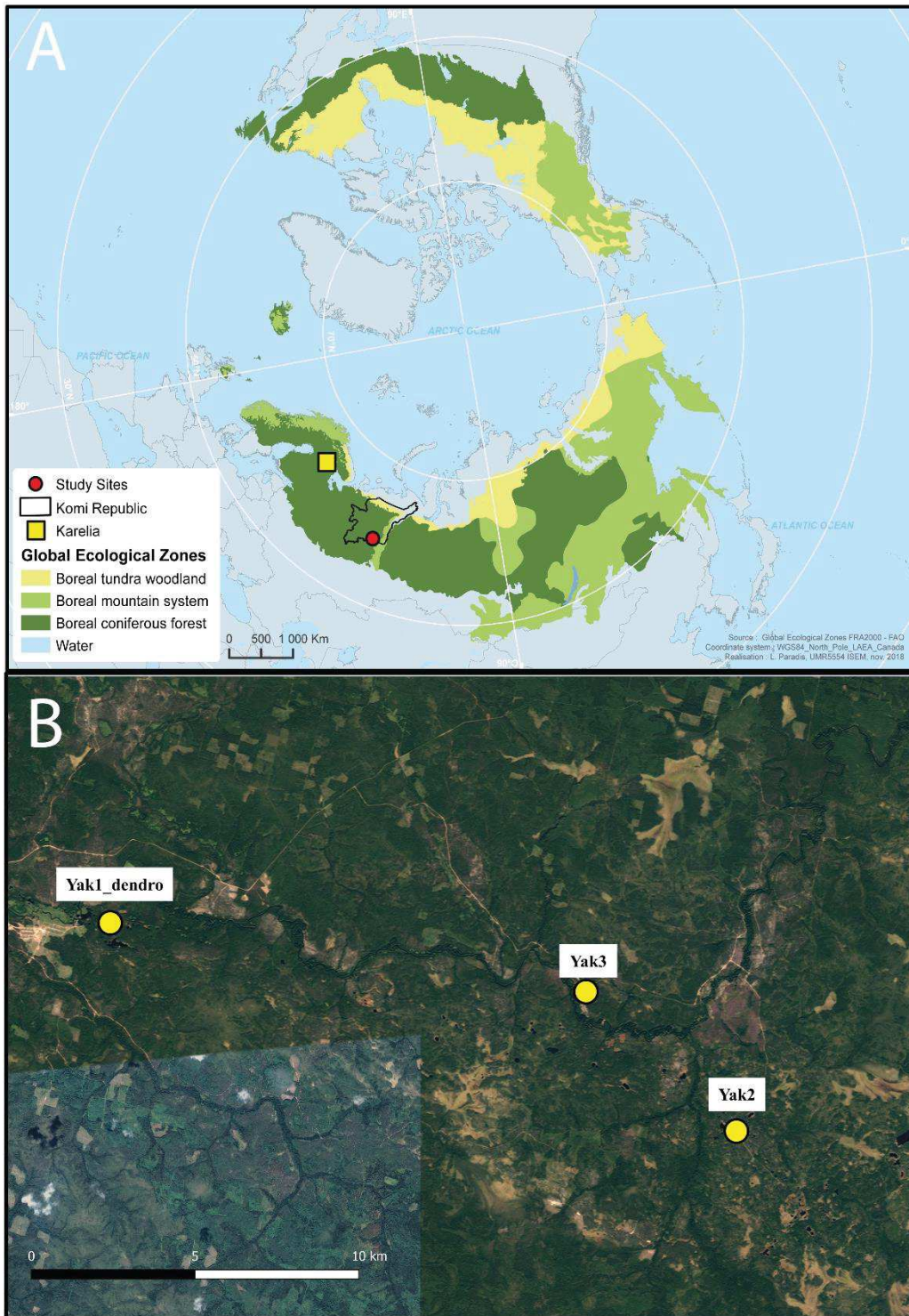


Figure II.1: A: Polar view of the extent of the boreal forest and location of the Komi Republic and the study area. B: Study sites. Detail of dendrochronological samples by site in Figure A 4.

2.2.2. The study sites

The Ural region is divided into sub-regions based on topography, from north to south: the polar Ural, pre-polar Ural and northern Ural regions. The study sites named Yak1_dendro, Yak2 and Yak3 (unofficial names) are located in the northern Ural region, 200 km east of Syktyvkar (Figure II.1; Figure A 3; Tableau 1). They correspond to forested peatland with *Pinus sylvestris* and *Betula pubescens* stands (Figure II.1, Figure A 3). Because cores from the same peatland area can record different fire histories (van Bellen et al., 2012), we developed a multi-site approach in order to provide a more holistic view of the fire history (van Bellen et al., 2012). Yak1_dendro was peatland around which only dendrochronology sampling was carried out, and no peat coring took place. A few kilometers away (14 and 19 km, respectively), the two other peatlands, Yak2 and Yak3, were cored. Two different cores were collected from site Yak2: core Yak2-A at the center and core Yak2-B at the periphery level, 270 m from core Yak2-A. Similarly, Yak3 provided 2 other cores: Yak3-A in the center and Yak3-B at periphery level) (Figure II.1; Tableau II.1), separated by about 250 meters. The cores were taken using an 8-cm diameter Russian peat corer.

Tableau II.1 : The main characteristics of the three study sites in the Komi Republic

	Yak1_dendro	Yak2-A	Yak2-B	Yak3-A	Yak3-B
Latitude	61°44'53.73" N	61°41'46.30"N	61°41'50.80" N	61°43'53.15"N	61°43'57.40"N
Longitude	55°15'0.04"E	55°34'27.60"E	55°34'28.30" E	55°29'39.6"E	55°29'30.70"E
Elevation (m a. s. l.)	132	140	140	131	128
Current local vegetation	<i>Pinus sylvestris, Picea abies s.l., Betula spp., Populus tremula, Larix sibirica, Abies sibirica, Sorbus aucuparia, Juniperus spp., Salix spp., Vaccinium uliginosum</i>	<i>Pinus sylvestris, Picea abies s.l., Betula spp., Populus tremula, Chamaedaphn e calyculata, Carex spp., Vaccinium uliginosum</i>	<i>Pinus sylvestris, Picea abies s.l., Betula spp., Populus tremula, Chamaedaph ne calyculata, Carex spp., Vaccinium uliginosum</i>	<i>Pinus sylvestris, Picea abies s.l., Betula spp., Populus tremula, Chamaedaphn e calyculata, Carex spp., Vaccinium uliginosum</i>	<i>Pinus sylvestris, Picea abies s.l., Betula spp., Populus tremula, Chamaedaphn e calyculata, Carex spp., Vaccinium uliginosum</i>
Peatland surface (ha)	1.88	4	4	2.4	2.4

Length of organic core (cm)		168.5	171.5	350	187.5
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2.2.3. Dating and chronologies of the peat cores

For each core, the chronology was based on five to seven radiocarbon measurements taken from charcoal particles, plant macroremains and bulk peat sediments, when sufficient macro-remains were not available (Tableau II.2). The charcoal sample was used for the Yak2-A site and allowed the oldest dating of this core. Significant differences in dates may appear between the different materials. Especially with regard to charcoal particles, which could come from old trees (more than 200 years old) and therefore have an "in-built age" effect (Oswald et al., 2005). However, in the case of peatlands and macrocharcoal, the timelapse due to migration in the peat recording is probably very small (unlike what sometimes happen in lakes (Oswald et al., 2005)). Whenever possible, we used macro-remains. When this was not possible, we used peat sediment samples directly from organic gyttja. The use of this panel of material for ¹⁴C dating has been realized in many studies in boreal regions (Ali et al., 2009a; van Bellen et al., 2012; Ouarmim et al., 2014). The radiocarbon dates were calibrated using the R package CLAM 2.2 (Blaauw, 2010), IntCal13 was used for the calibration curve (Reimer et al., 2013), and the NH1 post-bomb calibration curve was used for modern radiocarbon (Hua et al., 2013). A smooth spline function was used to fit the four age models (Blaauw, 2010) with a 0.95 confidence interval.

2.2.4. From charcoal particles to fire frequency reconstruction

In the laboratory, each peat sequence was divided into 0.5-cm slices. A 1-cm³ subsample was then taken from the center of each slice. These subsamples were soaked in 25 ml bleach with 3 g NaPO₃ and 0.5 g KOH, for at least 24 h on an agitator (Carcaillet et al., 2001). Then the material was gently rinsed through a 160-µm sieve. Commonly, in boreal zone affected by crown and severe wildfires a bigger sieve is used (> 300 µm) to collect charcoal particles from peat deposits, notably to infer *in situ* fire events (van Bellen et al. 2012; Adolf et al. 2018). In

our case, with surface fires and expected low concentration of charcoal into sediments, we securely used a 160 μm even if long distance transportation of charcoal particles could have been occurred (Oris et al., 2014). Nevertheless, several studies conducted in lake sediment deposits have shown that this charcoal particle size was mostly associated to local fire events, between 0-1km from the coring point (Higuera et al., 2007b; Ali et al., 2009a; Oris et al., 2014). The charcoal particles were counted and measured under a 20 \times stereo microscope and equipped with a digital camera connected to an image-analysis software system (WinSEEDLETM software; Regent Instruments Inc., <http://regent.qc.ca/>). We used the area measurement, notably in regard to Ali *et al.*, (2009) which concluded that area or count measurements display comparable fire history if locally-defined threshold is used to infer fire events. Charcoal measurements are reported as charcoal accumulation rates (CHAR, $\text{mm}^2 \text{cm}^{-2} \text{yr}^{-1}$) based on numerical age/depth models.

To linearize the results because of varying sedimentation rates, individual CHAR series were interpolated using a constant time resolution corresponding to the median sample resolution of each peat sequence (Higuera et al., 2011). Statistical analyses were performed using the CharAnalysis program (Higuera et al., 2009), <http://CharAnalysis.googlepages.com>), following the method used by Brossier et al. (2014). The CHAR series comprise low-frequency (background; $C_{\text{background}}$) and peak (or residual series; C_{peak}) components. We estimated $C_{\text{background}}$ with a robust Lowess using a 300–500 years window width, corresponding to the most suitable window for which signal-to-noise Index (SNI, signal strength relative to accompanying noise) was the best (cutoff value of $\text{SNI} = 3$) (Kelly et al., 2011; Brossier et al., 2014). C_{peak} values were obtained by subtracting $C_{\text{background}}$ from $C_{\text{interpolated}}$, which corresponded with a resampled record of the CHAR series. We then divided the C_{peak} series into two subpopulations: (i) noise, which represented variability in sediment mixing, sampling and noise induced by numerical analyses; and (ii) fire events (C_{fire}), representing fires occurring 0–1 km from the peat core sites (Lynch et al., 2004a; Higuera et al., 2007b). For each sample, we used a Gaussian mixture model to identify the noise distribution, with a 99th percentile threshold for separating samples into fire and non-fire events (Higuera et al., 2007b). The fire return interval (hereafter FRI) values, which corresponded to the time-span between two consecutive fire events, were obtained from the raw C_{fire} series. A Kernel density function (Mudelsee et al., 2004) was used to compute a temporally smoothed FRI. All analysis were conducted using the softwares *taust* (Mudelsee, 2002), *kernel* (Gasser and Müller, 1979, 1984) and *redfit* (Schulz and Mudelsee, 2002). The mean FRI (hereafter mFRI) was determined to reconstruct fire

history at regional spatial scale (Gavin et al., 2006; Courtney Mustaphi and Pisaric, 2013). The mFRI was made on the basis of pooled FRI for all peat sequences, and the 90% confidence intervals were calculated from the true distribution of the 1000 resampled FRI series, and are presented for a 300-year bandwidth. Significance between each millennia was also assessed using box-plot analysis and Wilcoxon rank sum test.

2.2.5. Tree-ring records of fire history

To establish a master chronology, we sampled tree-rings from trees that did not show fire scars, around the Yak1_dendro, Yak2 and Yak3 sites (Table A 1). Then, to evaluate the fire activity from tree rings, we sampled trees that had at least one fire scar. Within each site, the sampling took place within 200 m of the peatland shores (Brossier et al., 2014). A partial cross-section was taken as close to the root collar as possible, to date the establishment of the fire scars (Arno and Sneek, 1977). We sampled 14 cross-sections from dead and living pine wood (*Pinus sylvestris*) at Yak1_dendro, 18 from Yak2 and 34 from Yak3. For each sampled tree, the diameter at breast height, spatial coordinates and orientation of the scars were recorded. The preparation and analysis of the samples followed standard methods (Cook and Kariukstis, 1990). The cross-sections were allowed to dry for several days, and sanded using a progression of sandpaper grits from P80 to P600 (Schweingruber et al., 1988; Brossier et al., 2014).

Tree-ring analysis was carried out using a binocular microscope (Leica M80) according to standard dendrochronological methods (Niklasson et al., 2010; Stokes and Smiley, 1968). Pointer years (narrow, wide, incomplete growth rings, fire scars) were identified visually and used for cross-dating on living trees (Schweingruber et al., 1990). Tree-ring widths were measured along two radii using LINTAB 6. For dead trees, the tree-rings were counted and measured along two radii. Cross-dating was achieved using TSAPWin 4.80 software (Rinn, 2012). The same software was used for verification of cross-dating accuracy. For all scars, the calendar date was recorded. A fire event was validated when at least three trees had a fire scar dated to the same year.

2.3. RESULTS

2.3.1. Age models and chronologies

The peat cores measured 168.5 cm from Yak2-A, 171.5 cm from Yak2-B, 350 cm from Yak3-A and 187.5 cm from Yak3-B. For Yak-2A the date 7605 yr BP (Tableau II.2) was rejected by the best-fit age-depth model reflecting the sedimentation pattern (Blaauw, 2010). Based on the different age models (Figure II.2), the Yak2-A core covers almost the entire Holocene period, from 11015 to -58 cal. yr BP, with a mean temporal resolution of approximately 65 yr cm⁻¹ (standard deviation ~ 29 years). The Yak2-B core represented the last 9750 years, with a mean temporal rate of 57 yr cm⁻¹ (standard deviation ~ 24 years). Yak3-A and Yak3-B represented the mid-Holocene to the present day, 6000 and 4619 cal. yr BP to 0 and -65 cal. yr BP, respectively. The Yak3-B core had a mean temporal resolution of approximately 25 yr cm⁻¹ (standard deviation = 11 years), and Yak3-A 19 yr cm⁻¹ (standard deviation ~ 10 years). Therefore the Yak3-A and Yak3-B sequences displayed a finer time resolution from the mid-Holocene to the present day, compared with the other sequences.

Tableau II.2 : AMS ¹⁴C dating from Yak2-A, Yak2-B, Yak3-A and Yak3-B

Site	Laboratory. code	Depth (cm)	¹⁴ C yr BP (± σ)	Materials dated
Yak2-A	ULA-6948	5-5.5	325 ± 15	Plant macroremains
Yak2-A	ULA-6958	45-46	1455 ± 15	Bulk
Yak2-A	ULA-6966	85-85.5	3795 ± 15	Bulk
Yak2-A	ULA-6959	124.5-125	5415 ± 20	Bulk
Yak2-A ^a	ULA-6960	163-163.5	7605 ± 20	Bulk
Yak2-A	BETA-455694	165-165.5	9410 ± 30	Charcoal
Yak2-B	ULA-7050	5-6	1130 ± 15	Bulk
Yak2-B	ULA-7051	41-41.5	1785 ± 15	Bulk
Yak2-B	ULA-7052	77-78	3275 ± 15	Bulk

Yak2-B	ULA-7053	113-113.5	4505 ± 15	Bulk
Yak2-B	ULA-7054	149-149.5	7090 ± 20	Bulk
Yak3-B	ULA-6970	5-5.5	90 ± 15	Plant macroremains
Yak3-B	ULA-6961	49-49.5	1410 ± 20	Plant macroremains
Yak3-B	ULA-6962	92.5-93.5	2000 ± 15	Bulk
Yak3-B	ULA-6972	137-137.5	2500 ± 15	Plant macroremains
Yak3-B	ULA-6963	181-181.5	3905 ± 15	Bulk
Yak3-A	ULA-6967	5-5.5	360 ± 15	Plant macroremains
Yak3-A	ULA-6965	63-63.5	1815 ± 20	Bulk
Yak3-A	ULA-6964	121-121.5	2370 ± 20	Plant macroremains
Yak3-A	ULA-6971	179-179.5	2835 ± 15	Plant macroremains
Yak3-A	ULA-6968	237.5-238.5	3330 ± 15	Bulk
Yak3-A	BETA-455692	298.5-299	4880 ± 30	Bulk
Yak3-A	BETA-455693	326-326.5	5280 ± 30	Bulk

^aAge rejected by the age-depth model

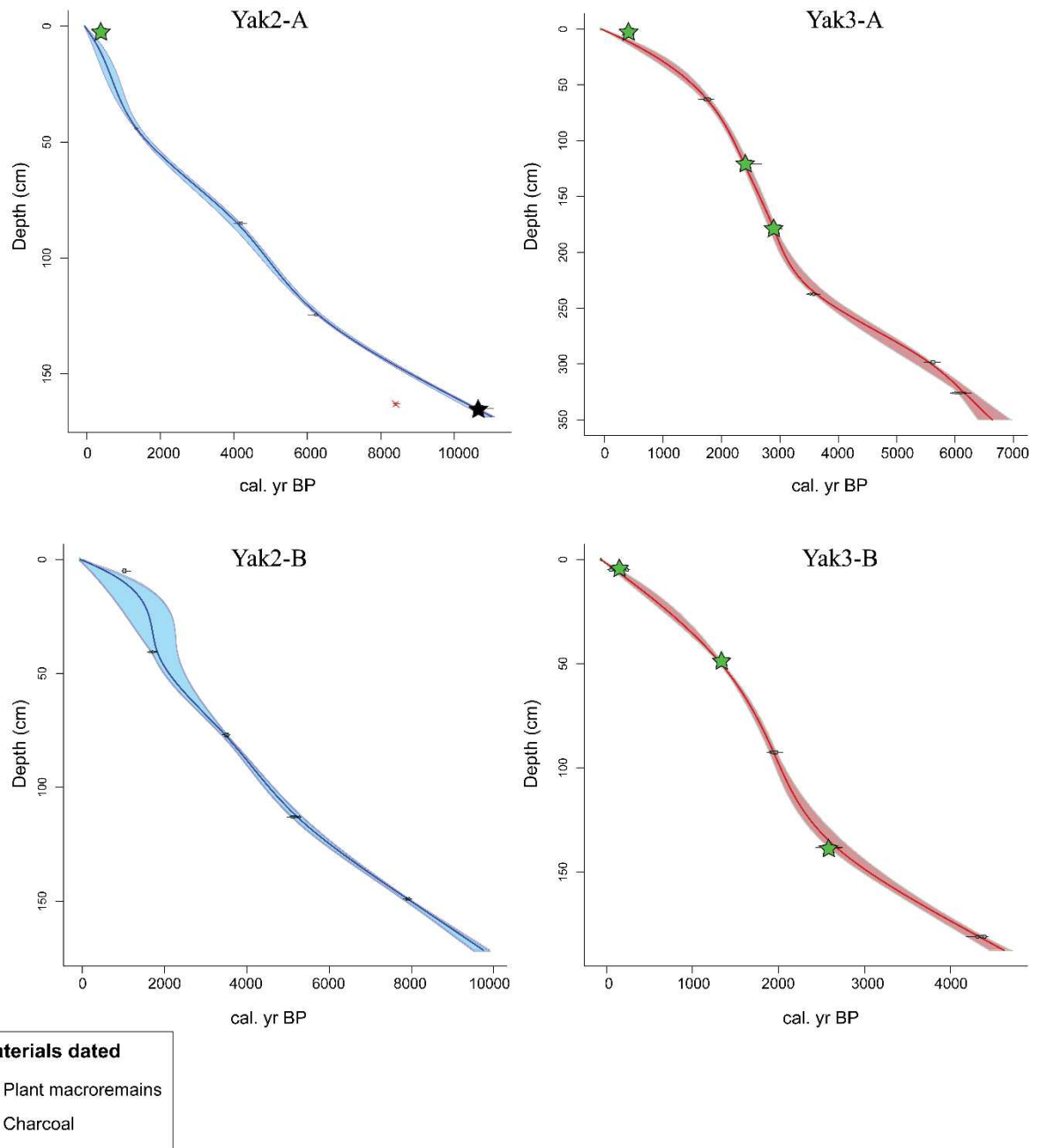


Figure II.2 : Age-depth model based on radiocarbon ages (see Table II.2) from Yak2-A, Yak2-B, Yak3-A and Yak3-B cores. The materials dated to ^{14}C are bulk (single black lines), plant macroremains (green stars), macrocharcoal (black star).

2.3.2. Fire history

2.3.2.1. Charcoal data

The charcoal analysis from Yak2-A indicated that the FRI fluctuated at around 500 years (median value 387 years) from 11000 to 8000 cal. yr BP (Figure II.3), then decreased rapidly until 7000 cal. yr BP, when values oscillated around 250 years. The FRI then remained stable before decreasing again after 1000 cal. yr BP to the present day, with values falling to about 100 years (Figure II.3). Yak2-B showed a different trend, with a slight increase in FRI during the Holocene, starting at around 200 years from 9000 cal. yr BP and reaching values close to 300 years at 450 cal. yr BP (Figure II.3).

For Yak3-B, the FRI fluctuated around 130 years between 4500 and 900 cal. yr BP, then reach values close to 95 years at present (Figure II.3). For Yak3-A, there was a sharp decrease in FRI between 6000 and 4000 cal. yr BP, dropping from 200 to 70 years.

These results indicate a spatial variability in the fire records, inferred from very close sequences. Despite this variability, the pooled reconstruction (mFRI) displayed a consistent decrease in FRI over the last 10000 years (Figure II.4). Between 11000 and 5100 cal. BP, the mFRI was above 200 years (range 600 to 200 years). After 5100 cal. BP (excepted for 1000 cal. BP), a gradual increase in fire frequency was recorded, with mean FRI reaching values below 200 years (range 200 to 40 years). Nowadays (since CE 1500), a fire activity with a mean FRI below 100 years was recorded. However, before 6000 cal. yr BP only Yak2-A and Yak2-B contributed to the reconstruction of the mFRI; for the period from 4500 cal. yr BP to the present day, the mFRI was based on all sequences. The CHAR outputs for each sequence are presented in the Appendix (Figure A 1). Limiting the analysis to 4600–0 cal. yr BP, which included the four chronosequences, confirmed a trend of decreasing FRI (Figure A 2).

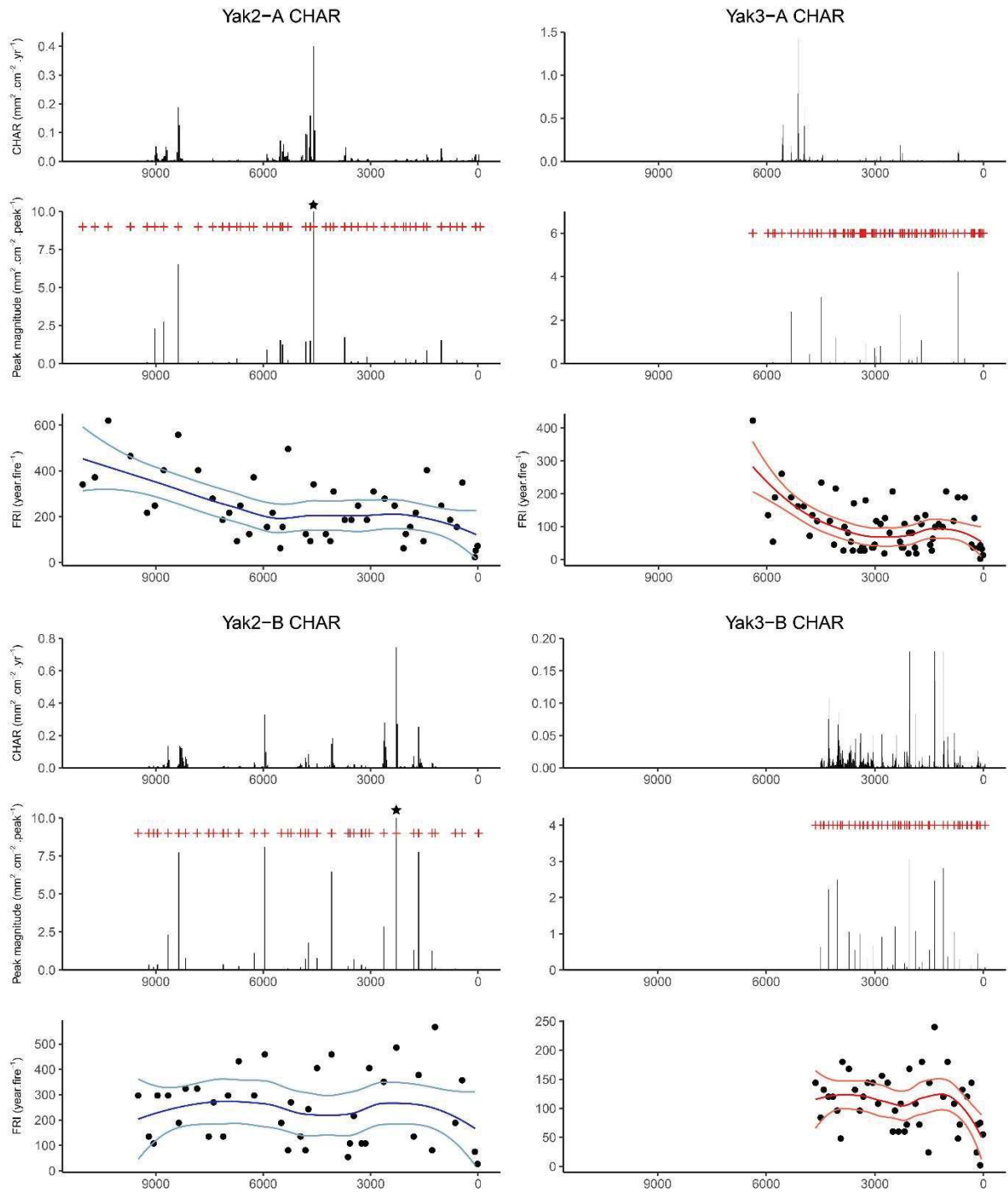


Figure II.3: CharAnalysis results: interpolated charcoal accumulation rate, peak magnitude and Lowess smoothed FRI for Yak2A, Yak2B, Yak3A and Yak3B. Red crosses are years with a fire event and black stars correspond to peak magnitude $>10 \text{ mm}^2 \text{ cm}^{-2} \text{ peak}^{-1}$ ($11 \text{ mm}^2 \text{ cm}^{-2} \text{ peak}^{-1}$ for Yak2A and $19 \text{ mm}^2 \text{ cm}^{-2} \text{ peak}^{-1}$ for Yak3B).

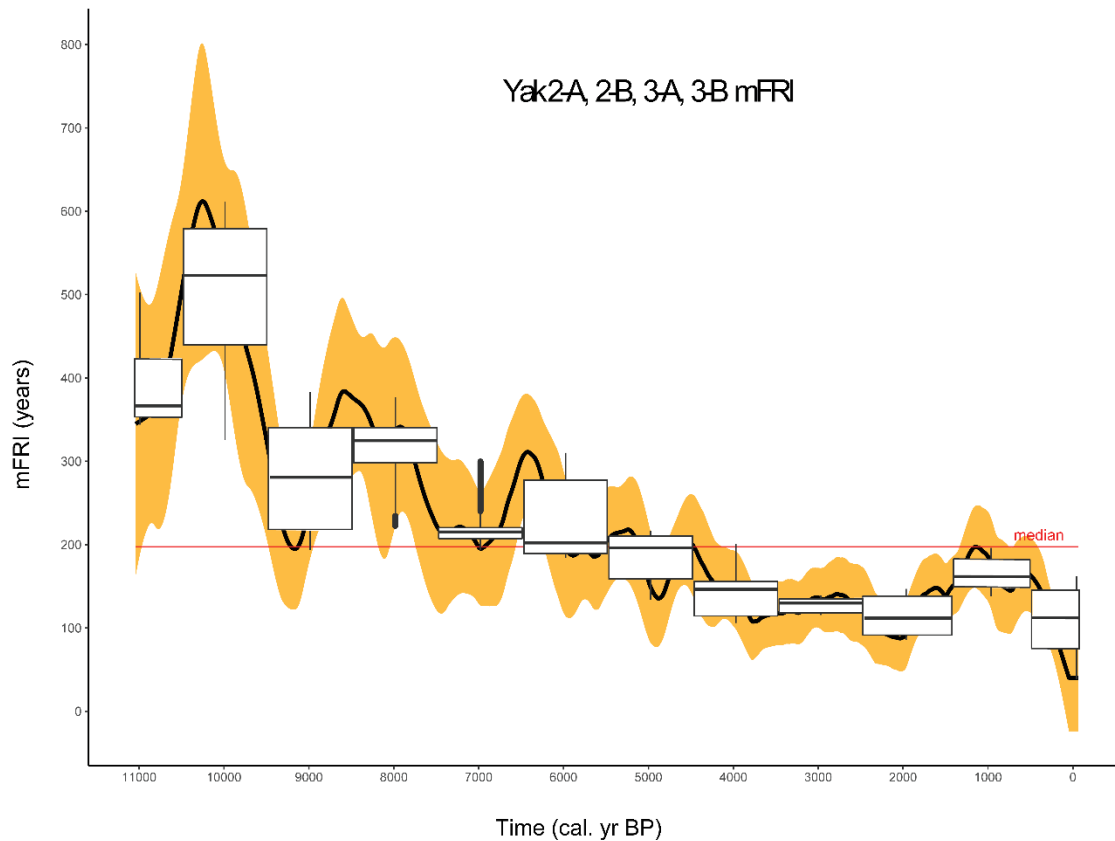


Figure II.4: Pooled FRI reconstruction (mFRI) from Yak2-A, Yak2-B, Yak3-A and Yak3-B cores. The red line represents the median of the mFRI (197,29 years). Orange shaded area is confidence interval. Detected trends are showed by box-plot analysis carried out for each 1000 years period (except for extremities) significance between millennia was assessed using the Wilcoxon rank sum test.

2.3.2.2. Dendrochronology data

In total, we dated 122 fire scars from live and dead pine woods within the three sites (Figure II.5). The six main fires (present on at least on three trees) were dated to 1791, 1851, 1861, 1868, 1917 and 1936 yr CE (Figure II.5). Fire events in 1791, 1851 and 1917 yr CE were detected at Yak2. Fire events in 1861 and 1936 yr CE were common across the three sites. A fire event in 1868 yr CE was common to Yak1_dendro and Yak3. At Yak1_dendro, the fires in 1861, 1868 and 1936 yr CE provided a mean FRI of 37 years. At Yak2, the fires in 1791, 1851, 1861, 1917 and 1936 yr CE provided a mean FRI of 36 years. At Yak3, the fires in 1861 and 1936 yr CE provided a 75-year FRI (Tableau II.3).

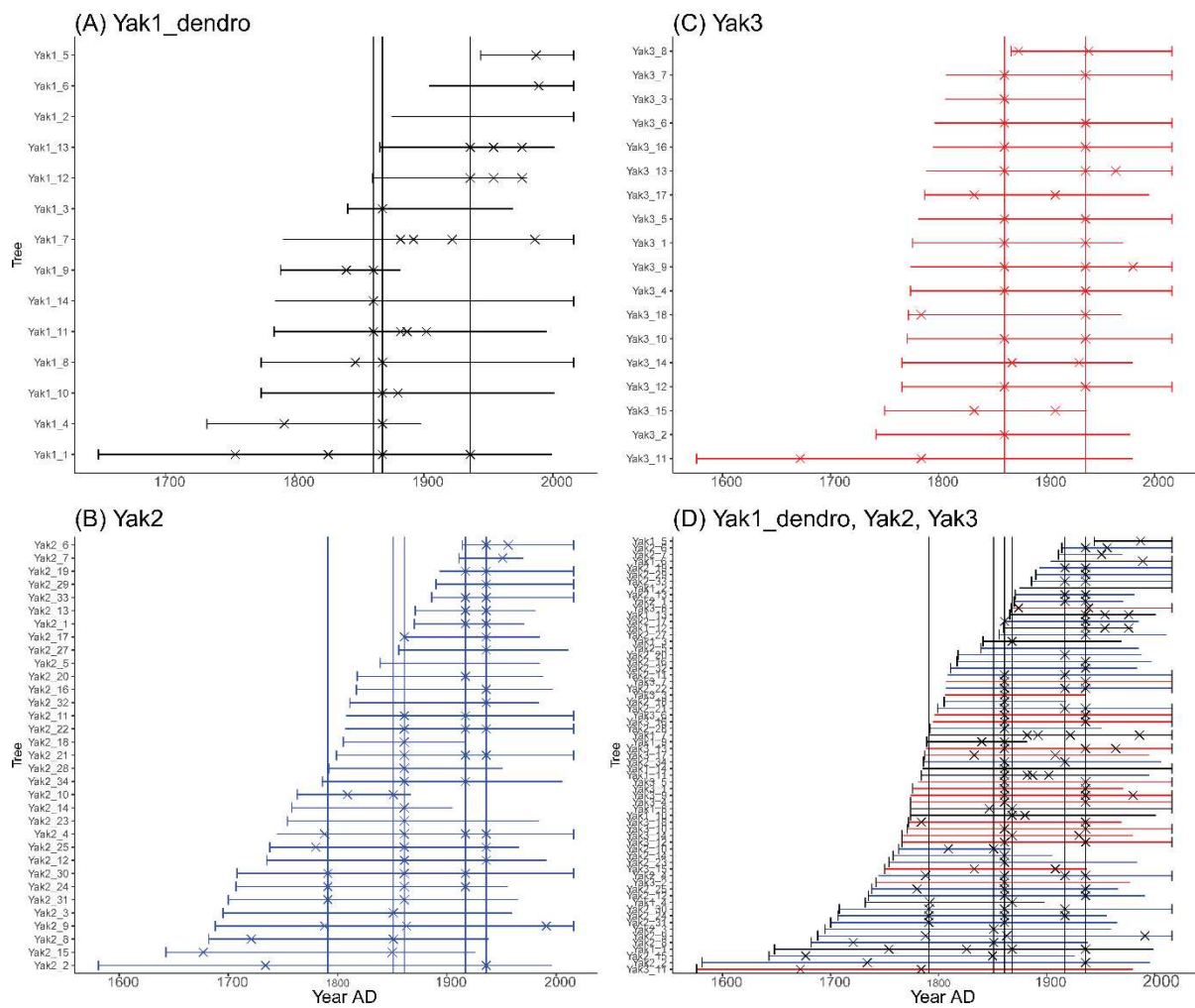


Figure II.5: Tree-ring records of fire activity. Each horizontal line is an individual tree. (A) Yak1_dendro; (B) Yak2; (C) Yak3; (D) The three sites together. Black horizontal lines indicate Yak1_dendro, red horizontal lines Yak3 and blue horizontal lines Yak2. Black crosses represent fire scars. Vertical gray bands indicate obvious fire events defined visually.

Tableau II.3: Results of dendrochronological analyses

Site	Yak1_dendro	Yak2	Yak3
Dates of fires (CE)	1861, 1868, 1936	1791, 1851, 1861, 1861, 1936 1917, 1936	1861, 1861, 1936
Fire return interval (FRI) (years)	37 years	36 years	75 years

2.4. DISCUSSION

2.4.1. Spatial variability in fire activity

Yak2-A, Yak3-A and Yak3-B showed a decrease in FRI during the Holocene, while Yak2-B showed a slight increase. This discrepancy demonstrates the importance of conducting multi-site analyses in order to have a synthetic view of fire history at local spatial scale. However, such differences in fire history from the same peat deposit are not surprising, and have been observed in several regions dominated by boreal forests (van Bellen et al., 2012). In eastern Karelia, Kuosmanen et al. (2014), also showed differences in fire activity across the Holocene at local spatial scale: three sites were analysed, separated by 800m and 70km. Yet the three sites have a completely different fire history. Other studies in boreal zone have shown that there may be significant differences between fire histories at a local scale (Gavin et al., 2006; Ohlson et al., 2011; Genries et al., 2012). There are several possible explanations for this. Firstly, within a peatland, local humidity can have high spatial variability (Zoltai et al., 1998; Hellberg et al., 2004; van Bellen et al., 2012). This explains that some areas of the peatland can be wet while others are dry. This can in turn lead to high spatial variability in fire propagation (Zoltai et al., 1998). Secondly, peatland vegetation can have a strong impact on the spread of fire, in particular the presence and distribution of shrubs and trees within the peatland (Camill et al., 2009). Thirdly, fires in the Russian boreal forests are mainly surface fires (Soja et al., 2007; Gauthier and Vaillancourt, 2008), and such fires tend to be scattered and burn forest litter, shrubs and the bases of trunks (Zoltai et al., 1998).

The dendrochronological fire reconstruction also revealed differences within and between the three sites. The Yaksha River separates the sites, thus providing a natural barrier to the spread of fire from Yak1_dendro to Yak2 and Yak2 to Yak3. Some fires were recorded at all three sites (such as in 1861 and 1936) and some only at two sites (such as in 1868). Finally, three fires were found only on one site (1791, 1851 and 1917). Within each site, fires have affected some trees and not others. This could mean that a fire has occurred within the site but has not burned its entire surface, which is possible due to wind conditions and local topography

(Schweingruber et al., 1988; Kulakowski and Veblen, 2002; van Bellen et al., 2012). These results again underline the fact that using a multi-site approach and different proxies are necessary to obtain an overview of fire activity than using only one site and only one core (Rius et al., 2011).

In order to provide an overall view of the FRIs from our study area, we pooled the four cores using a Kernel density function (Figure II.4), which took into account inter-site variability and provided a confidence interval for evaluating whether the observed trends were significant (Mudelsee et al., 2004). Fire activity from before 6000 cal. yr BP was only determined with results from the two cores Yak2-A and Yak2-B. Additional sites need to be studied to provide a more detailed view of fire activity for this period. However, it is clear that during the first half of the Holocene fire activity was much lower than after 5000 cal. yr BP, and a generally decreasing trend in mFRI was recorded over the Holocene. The mFRI decreased from almost 600 years at *c. (circa)* 10000 cal. yr BP to less than 100 years at present (Figure II.4). The boxplots highlight the progressive decrease in mFRI and the Wilcoxon test showed that the decrease is significant each millennium ($p\text{-value} = 5.723\text{e-}06$).

Fire scars on a tree trunk and trapped charcoal in sedimentary deposits are both different indicators of a fire event. A charcoal peak identified from sedimentary CHAR series can come from one or more fires, with a spatial scale of about 0 to 1 km (Higuera et al., 2007b) but nevertheless mild to low severity fires, as surface fires generally are, may be more difficult to detect in sediment records, while a fire event dated by dendrochronology represents only one fire at the spatial scale of the tree and is more accurate (Higuera et al., 2005; Brossier et al., 2014; Oris et al., 2014). Spatial variability is greater with charcoal proxies than with dendrochronology. The complementary use of these two proxies allows fire events to be detected more clearly, as shown in Brossier et al. (2014), and Waito et al. (Waito et al., 2018), around lakes in Canadian boreal forest. In our study, FRI values from charcoal series, oscillating between 100 and 40 years for the last 300 years, are of the same order of magnitude as dendrochronological analyses, which provided FRI values of less than 100 years at all three sites. The present-day mFRI determined by both the charcoal and dendrochronological analyses is by far the lowest recorded over the last 10000 years from our study area.

It is possible that at the local level, fire dynamics are not linked to the climatic driver because of the topographic, vegetation and soil variables that may be more important at these scales. Studies by Kuosmanen et al. (2014 and 2016), on fire-vegetation interactions at the local scale, based on the study of three hollows in Karelia (west of the Komi Republic) did not show strong

links between fire dynamics (which differed from one site to another) and climate or vegetation during the Holocene. However, it may be interesting to discuss the overall decline of the FRI in our study site. Climate, vegetation and human activity factors are, initially, the three tracks that can be explored (Johnson, 1992; Swetnam, 1993; Gauthier and Vaillancourt, 2008; Power et al., 2008; Flannigan et al., 2009). An increase in fire activity during the Holocene has also been observed for northern extratropics (Figure II.6A) (Marlon et al., 2016), Sweden from 4000 cal. yr BP (Figure II.6B) (Drobyshev et al., 2016) and all of Fennoscandia and Denmark (Figure II.6C) (Clear et al., 2014.). It is important to keep in mind that, the decrease in mFRI in our study corresponds with an increase in the influx of charcoal in others.

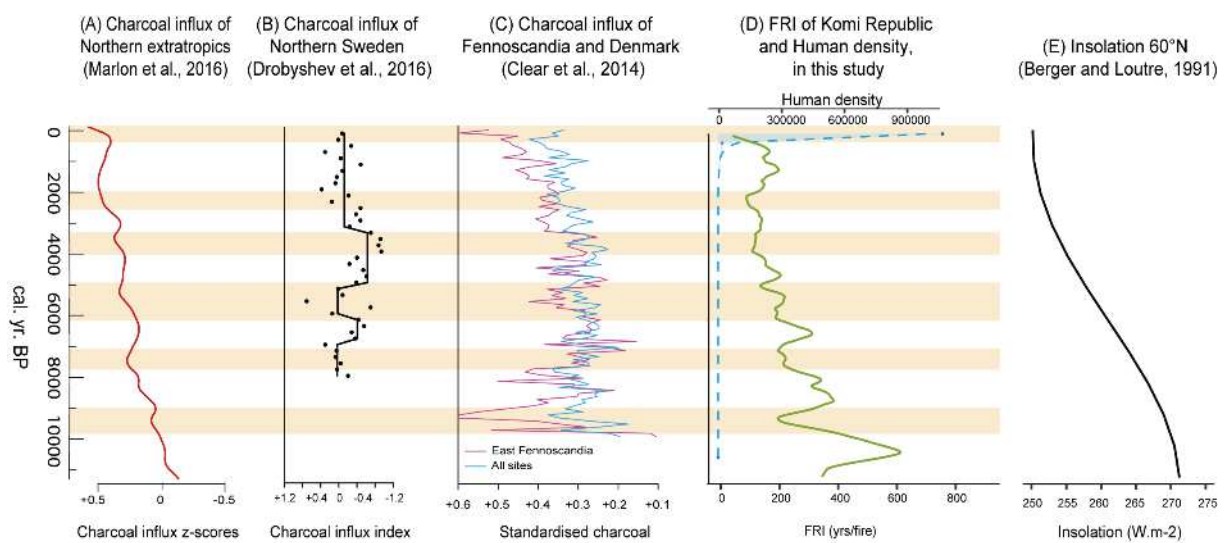


Figure II.6: Proxies for Holocene fire history along a west–east transect from northern Sweden to the Komi Republic (A, B, C, and D). (A) Charcoal influx in the northern extratropics (Marlon et al., 2006) shown by z-score: an increase in the z-score represents an increase in fire activity. (B) Charcoal influx in northern Sweden (Carcaillet et al., 2007; Drobyshev et al., 2016). (C) Charcoal influx in Fennoscandia and Denmark (Clear et al., 2014). (D) FRI and human population density in Komi Republic (this study). (E) Insolation at latitude 60°N (Berger and Loutre, 1991). Yellow bands correspond to synchronized trends

2.4.2. Climatic imprint

Trends in fire activity may be related to climate change, as shown by Marlon et al. (2016) (Figure II.6A) which associated their results showing an overall increase in fire activity across the Northern Hemisphere with an increase in temperature, carbon dioxide concentration and biomass for the Northern Hemisphere. In the same way, Drobyshev et al. (2016) showed that the increase in fires in Sweden was related to cold and dry climatic conditions, which resulted from a decrease in the surface temperature of the Atlantic Ocean redirecting the activity of the prevailing westerly winds. Climatic reconstructions inferred from pollen, plant macrofossils, cladocera, chironomids and diatoms are available from North America and Arctic Canada (Ritchie et al., 1993; Gajewski, 2015; Bajolle et al., 2018), in the pre-polar region 380 km to the north of our study area (Kultti et al., 2003) and the polar Ural region 700–800 km to the north of our study area (Andreev et al., 2005; Salonen et al., 2011). In North America and Arctic Canada, an early Holocene thermal maximum (from about 8000 cal. yr BP to 5000 cal. yr BP) is evidenced with summer temperatures at least 2° warmer than today (Axford et al., 2009; Viau and Gajewski, 2009). In the pre-polar and polar Ural regions, the climate was probably moist and warm (summer temperatures *c.* 4°C warmer than today) between 8000 and 4500 BP (Kultti et al., 2003). In Arctic Fennoscandia, the influence of the Atlantic Ocean induced mostly colder climatic conditions during the early Holocene (Kullman and Kjällgren, 2000; Korhola et al., 2002; Seppä and Birks, 2002), while warmer conditions persisted in northern Russia and northern Europe (Tarasov et al., 2009; Elina et al., 2010; Mauri et al., 2015). After 4500 cal. yr BP, a gradual decrease in temperature occurred across most Arctic and boreal regions, corresponding to the Neoglacial period (4500-3000 cal. yr BP) in North America (Barber et al., 1999; Viau and Gajewski, 2009) and including the Little Ice Age (*c.* AD 1400). These climatic oscillations are notably associated with a gradual decrease in summer insolation (Berger and Loutre, 1991), (Figure II.6E). Closer to our sites, the study of the Vychegda River Basin (about 200 km west of our study area) by Sidorchuk et al. (2001) based on palynological analysis showed that onset of the Holocene, from 10000 cal. yr BP to 6000 cal. yr BP, climatic conditions were very continental, with temperatures much colder than today (-3.5°C to -2.5°C in January and -0.5°C in July). The climate was also wetter than today from 10000 cal. yr BP to 8400 cal. yr BP (more than 150 mm), then drier from 8400 cal. yr BP to 6000 cal. yr BP (-50 mm). From 6000 cal. yr BP to 0 ka, climate conditions were warmed, in summer first (up to + 2 ° C compared to today) and then in winter (+ 1 ° C). The precipitation weakly increased, especially in winter. In regard to the regional climate dynamic one can assume that the study zone, the low fire activity recorded between 10 000 and 6000 cal. yr BP,

could be due to conditions (cold and wet) less conducive to fire compared to after, with the gradual establishment of warmer conditions favorable to fire activity. However, the increase in humidity could have favored lightning (Lynch et al., 2004b; Veraverbeke et al., 2017), which is a natural cause of ignition source and increased the observed fire activity between 10000 and 8400 cal. yr BP (FRI increasing from more than 500 cal. yr BP to about 300 cal. yr BP). From 6000 cal. yr BP, the warmer temperatures, linked to slightly more humid conditions, were also favorable for fuel built (Amiro et al., 2001; Veraverbeke et al., 2017) and could explain the increase of fire activity recorded increase in fire activity observed. Climate can have a direct influence on fire activity, but also an indirect influence through vegetation dynamics (Higuera et al., 2008, 2009; Girardin et al., 2013; Goldammer, 2015).

2.4.3. Vegetation interactions

In boreal forest ecosystems, the vegetation composition is also related to the fire regime (Goldammer and Furyaev, 1996; Girardin et al., 2013). Over time, the climate can have an initial impact on the composition of the vegetation by promoting the development of some species under optimal conditions of temperature and humidity but preventing the development of some others (Higuera et al., 2009). This vegetation can then have an influence on fire activity for example, because of the soil moisture, the vulnerability of the lower branches (Goldammer and Furyaev, 1996; Girardin et al., 2013). During the early Holocene, around 10,000 cal. yr BP, a periglacial steppe forest system was present in the Vychegda River basin, less conducive to the spread of fires (Golubeva, 2008; Sidorchuk et al., 2001). This is in accordance with high FRI recorded at this time in Yaksha (more than 500 years). From 9300 cal. yr BP, spruce forests and hardwood (*Corylus* sp., *Ulmus* sp. and *Tilia* sp.) emerged, thanks to the warming of the climate and the increase in humidity (Sidorchuk et al., 2001; Giesecke and Bennett, 2004; Golubeva, 2008). At this time, FRI values (from about 280 years to 350 years) could favor species with low fire tolerance, such as spruce (Goldammer and Furyaev, 1996). From 8000 to 4600 cal. yr BP, where FRI decreased until 200 years, the spruce forest developed, but other species (pines, birches, firs and larches) also increased (Golubeva, 2008). The increase in fire activity has favored the emergence of tolerant and pioneering species, such as birches and pines (Goldammer and Furyaev, 1996), As well as the drier climate, for which pines are well adapted (Kullman, 1986). From 4600 to 2500 cal. yr BP, these spruce forests were progressively replaced by the light taiga, composed of pine forests (*Pinus sylvestris*), in association with

birches (*Betula* sp.), in line with the increase in temperatures (Goldammer and Furyaev, 1996; Golubeva, 2008). Both species are fire-resistant (Goldammer and Furyaev, 1996), which is coherent with the FRI recorded at this time (around 150 years). Since 2500 cal. yr BP, Golubeva (2008) documents the interruption of the light taiga by a phase of dark taiga between 1800 and 800 cal. yr BP, which is associated with a slight increase in temperatures and called the small climate optimum (Golubeva, 2008). At this time, FRI values increased around 200 years, reflecting the lower fire tolerance for these species (Goldammer and Furyaev, 1996). From 800 cal yr BP, the FRI decreased again to values around 50 years, which allowed the establishment of a light coniferous forest, composed mainly of pyrophytes such as *Betula* sp. and *Pinus sylvestris*, is compatible with low FRI (Sannikov and Goldammer, 1996; Hille and Den Ouden, 2004; de Groot et al., 2013) with FRI values recorded < 200 years. In this frame of natural and ecological dynamics link climate, vegetation and fire, human became more and more present in the study zone in the recent time.

2.4.4. Human impact

From the 10th century (around 800 cal. yr BP) to the end of the 19th century (around 1700 cal. yr BP), slash-and-burn agriculture was dominant in the Republic of Komi and other parts of Europe. The fire dynamics was obviously influenced by human being. Then, at the end of the 19th century, slash-and-burn agriculture was banned (Petrov, 1968), but farmers continued to practice it, without control increasing the probability of fires (Chernyakova, 2013). Archaeological data indicate that the first settlements in the territory date back 32-35 thousand years on the Pechora River (Taskaev, 2006). Then, the colonies also settled along large rivers. Most of the Republic's territory was practically undeveloped. In addition, the study area is directly adjacent to the UNESCO monument "Komi Virgin Forests". As a result, the region has hardly suffered any human influence (Taskaev, 2006). Although the region was sparsely populated at the beginning of the Holocene, the decline in FRI observed from 10000 to 9000 cal. yr BP (FRI around 500 years, decreased to less than 300 years), the Komi Republic may have been affected by hunter-gatherer communities that had a good command of the use of the forest and that may have had an impact on fire activity in the boreal forests, as shown by Kaplan et al., (2016) in Europe, at the beginning of the Holocene. During the last century, human activities have become the main source of fire ignition (an estimated 65% of effective ignitions) (Naryshkin, 2003) in the Komi Republic. Simulations of demography and migration during the

Holocene based on the History Database of the Global Environment suggest that human population densities have generally been relatively low and episodic in the Ural region during the Holocene (Karmanov et al., 2011a; Klein Goldewijk et al., 2011). Significant augmentation in human population density is recent, increasing by a factor of 100 over the last five centuries (Drobyshev et al., 2004a). Since the fifth century AD, the increase in human population with the development of slash-and-burn agricultural practices (Drobyshev et al., 2004a) have affected the fire activity of the area and could explain the very sharp decrease in FRI during the more recent period (the last 500 years), with values below 100 years.

2.5. CONCLUSION

Our study provides the first reconstruction of fire activity in the northern Ural region of the Holocene time period. The results, based on a multi-site and multi-proxy approach including charcoal and dendrochronological data, indicate a gradual decrease in FRI over the Holocene, in particular during the last 500 years. The causes of these fire dynamics are certainly multiple (climate, vegetation composition and human impact). The gradual establishment of warmer conditions from the mid-Holocene, especially during the summer, along with the development of a landscape including flammable conifers such as *Pinus sylvestris*, have probably both contributed to the increase in fire activity since 4600 cal. yr BP. Anthropogenic factors are probably associated with the rapid increase in fire frequency recorded recently (the last 500 years). The present-day fire activity is by far the lowest recorded over the last 10000 years from our study area. So, the addition of impact of current global warming with human being activities could lead to another increase of fire activity and the development of situations very far from the natural range of variability (600-200 FRI) recorded over the Holocene.

Acknowledgments

We thank M. Mudelsee for his training and advice on the statistical treatment of our data and S. Canal for his help and advice on charcoal counting. This research was funded by the Belmont Forum through the Agence Nationale de la Recherche (ANR) as part of the PRERREAL international research project (grant #292-2015-11-30-13-43-09 to ID), the Institut Universitaire de France (IUF) to Ali AA, and the state order to the Forest Research Institute of Karelian Research Centre Russian Academy of Sciences (FRI KarRC RAS). The study was conducted within the framework of the NordicProxy network, which is supported by the Nordic

Forest Research (SNS) and consortium GDRI Cold Forests. This is an ISEM contribution N°ISEM 2019-110.

2.6. ACKNOWLEDGMENTS

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2.7. APPENDICES

Table A 1: Geographical location of each dendrochronological sample

Site	Latitude	Longitude
Yak1_dendro_1	61.74929	55.22873
Yak1_dendro_2	61.7493	55.22884
Yak1_dendro_3	61.74893	55.22903
Yak1_dendro_4	61.7488	55.22922
Yak1_dendro_5	61.74904	55.22884
Yak1_dendro_6	61.74917	55.22887
Yak1_dendro_7	61.74981	55.22844
Yak1_dendro_8	61.7499	55.22826
Yak1_dendro_9	61.75003	55.22854
Yak1_dendro_10	61.75077	55.23019
Yak1_dendro_11	61.75084	55.23051
Yak1_dendro_12	61.75112	55.23059
Yak1_dendro_13	61.75131	55.23002
Yak1_dendro_14	61.75143	55.23011
Yak2_1	61.69495	55.57477
Yak2_2	61.69502	55.57498
Yak2_3	61.6951	55.57531
Yak2_4	61.69523	55.57465
Yak2_5	61.69558	55.57258
Yak2_6	61.69637	55.57367
Yak2_7	61.69617	55.57156
Yak2_8	61.6953	55.56931
Yak2_9	61.6952	55.56921

Yak2_10	61.69456	55.56897
Yak2_11	61.69395	55.56963
Yak2_12	61.69386	55.57186
Yak2_13	61.69421	55.57245
Yak2_14	61.69371	55.57324
Yak2_15	61.69356	55.57358
Yak2_16	61.69347	55.57384
Yak2_17	61.69296	55.57507
Yak2_18	61.69333	55.5756
Yak2_19	61.69438	55.57644
Yak2_20	61.6944	55.57689
Yak2_21	61.69453	55.57697
Yak2_22	61.69475	55.57683
Yak2_23	61.69492	55.57603
Yak2_24	61.69512	55.57902
Yak2_25	61.69557	55.57814
Yak2_26	61.696	55.57734
Yak2_27	61.69624	55.57744
Yak2_28	61.69694	55.57381
Yak2_29	61.69703	55.57388
Yak2_30	61.69767	55.57427
Yak2_31	61.69764	55.57453
Yak2_32	61.69707	55.5757
Yak2_33	61.69724	55.57622
Yak2_34	61.69718	55.57711
Yak3_1	61.73334	55.49385
Yak3_2	61.73293	55.49343

Yak3_3	61.73271	55.49438
Yak3_4	61.73228	55.49473
Yak3_5	61.73219	55.49484
Yak3_6	61.73225	55.49511
Yak3_7	61.73195	55.4949
Yak3_8	61.73196	55.49499
Yak3_9	61.73178	55.49424
Yak3_10	61.73154	55.49385
Yak3_11	61.7313	55.49396
Yak3_12	61.73037	55.49327
Yak3_13	61.73077	55.49218
Yak3_14	61.73048	55.49156
Yak3_15	61.73038	55.49056
Yak3_16	61.73046	55.49093
Yak3_17	61.73111	55.48955
Yak3_18	61.73324	55.4911

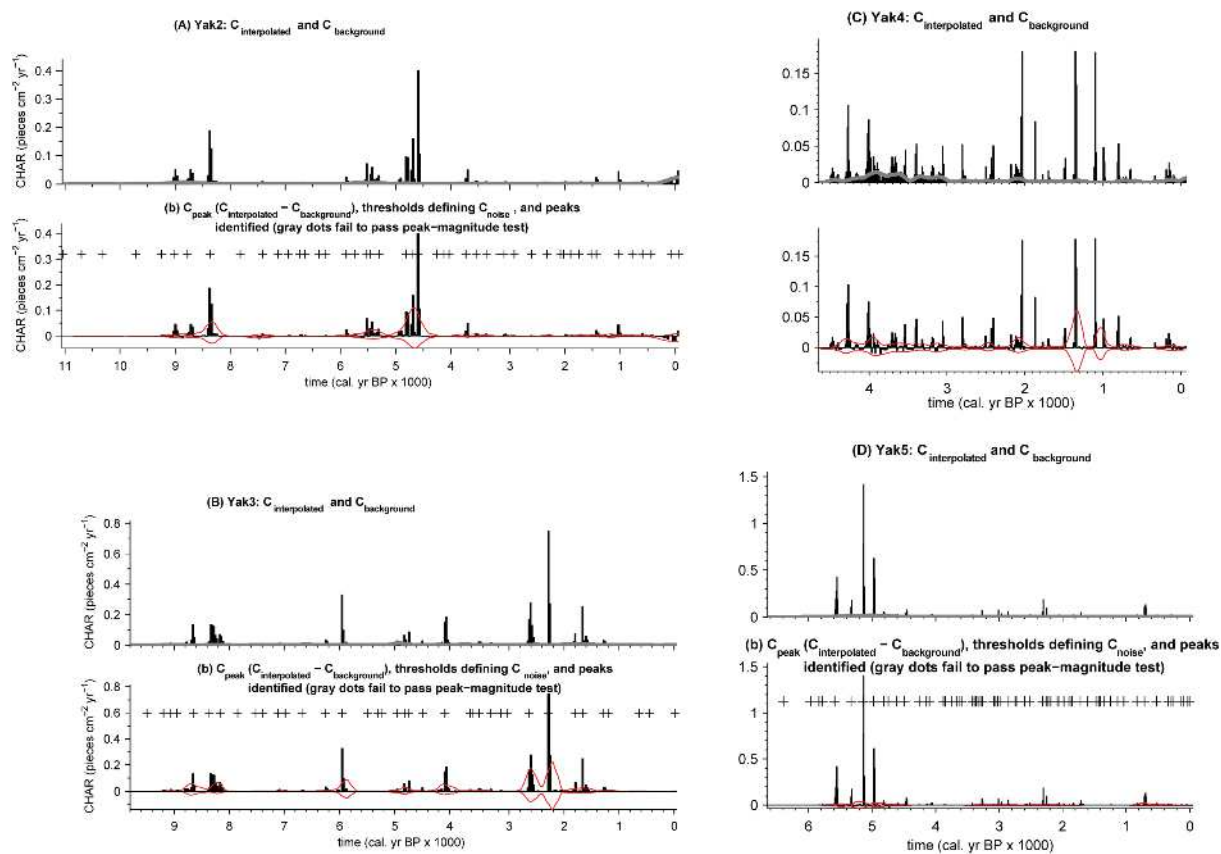


Figure A 1: Raw outputs of CharAnalysis representing $C_{background}$, $C_{interpolated}$ and the threshold (red line)

Yak2-A, Yak2-B, Yak3-A and Yak3-B mFRI common portion

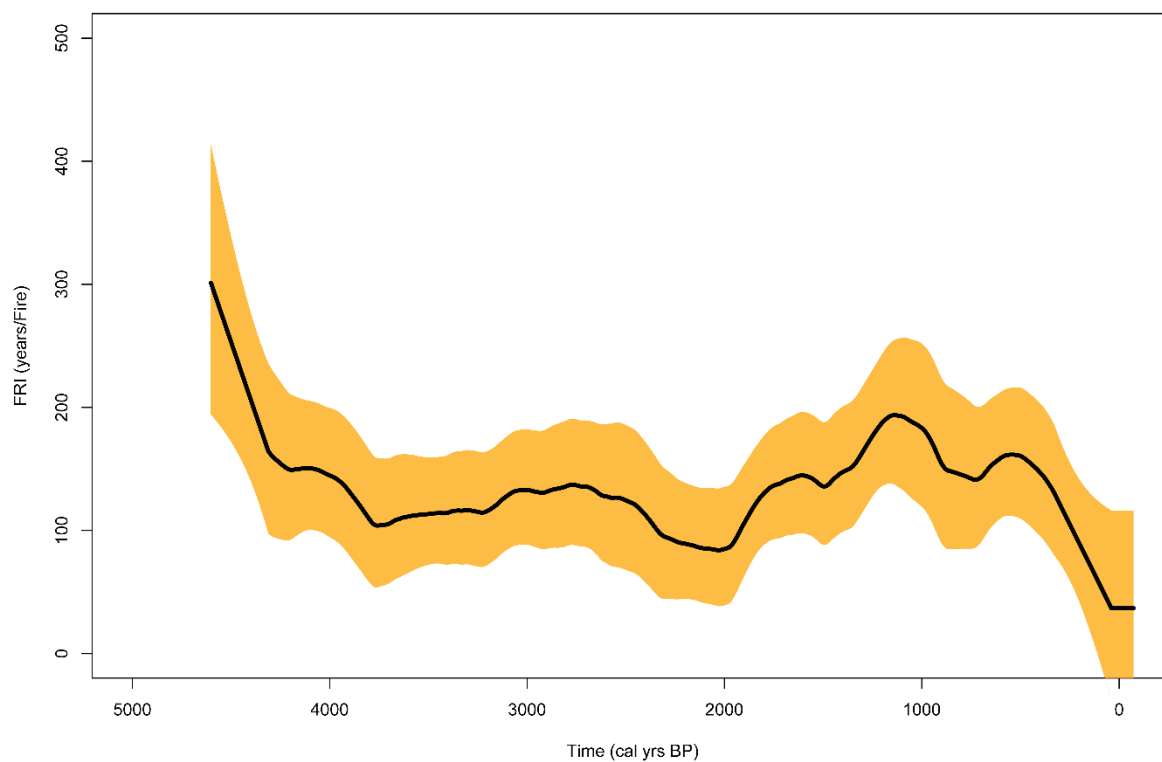


Figure A 2: Pooled FRI reconstruction (mFRI) of Yak2, Yak3 Yak4 and Yak5 sites on the common chronological portion. Shaded areas are confidence intervals



Figure A 3: Photo of the Yak2 forested peatland

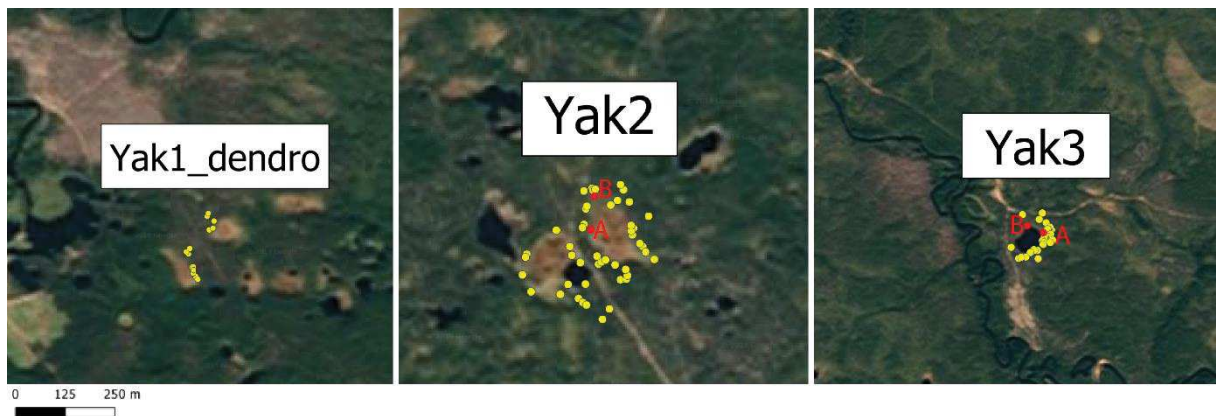


Figure A 4: Focus on each study area. The yellow dots represent the dendrochronology samples and the red dots represent the cores location.

Chapitre III.

LE FEU A-T-IL CONTROLE LA COMPOSITION DE
LA FORET BOREALE DE CONIFERES DANS LE
NORD DE LA REGION DE L'OURAL
(REPUBLIQUE DE KOMI, RUSSIE) ?

Did long-term fire control the coniferous boreal forest composition of northern Ural region (Komi Republic, Russia)?

Chéïma Barhoumi, Adam A. Ali, Odile Peyron, Lucas Dugerdil, Olga Borisova, Yulia Golubeva, Dmitri Subetto, Alexander Kryshen, Igor Drobyshev, Nina Ryzhkova and Sébastien Joannin

Journal Of Biogeography, soumis pour une troisième review

3.1. ABSTRACT

Aim Documenting past vegetation dynamics and fire-vegetation relationships at a regional scale is necessary to understand the mechanisms that control the functioning of the boreal forest (taiga in Russia), which is particularly sensitive to climate change. The objective of this study is to document these interactions in the Komi Republic during the Holocene.

Methods Two palaeoecological approaches are combined, based (1) on pollen (this study) and charcoal analysis (recomputed from our previous analysis) applied to cores from two peatlands and (2) on a REVEALS model (a part of the Landscape Reconstruction Algorithm “LRA”) applied to six regional pollen cores in order to obtain a regional estimate of vegetation cover during the Holocene.

Location Yaksha, Vychegda river basin of Southern Republic of Komi, Russia

Results The pollen diagram produced locally from Yaksha was compared with the regional vegetation cover determined by REVEALS. Taxa such as *Abies* sp. and *Pinus* spp. showed differences between the two approaches, but vegetation signals remain qualitatively consistent. From 10,000 to 6,000 cal. yr BP, the forest was mainly a light taiga (composed of *Pinus sylvestris* and *Betula* spp.) and low fire activity was recorded. From 6000 to 3500 cal. yr BP, a dark taiga (composed of *Picea* spp., *Abies sibirica* and *Pinus sibirica*) was established due to favourable climatic conditions, despite higher fire activity. From 3500 cal. yr BP onwards, the continuous increase in fire activity allowed for a gradual return of light taiga, *Betula* spp., likely reinforced by human activities. The dynamics of *Picea* spp. and *Abies* sp. were asynchronous between the sites. For *Picea* spp., the hypothesis of local inter-site expansion distributed along stream corridors is supported by the data. For *Abies* sp., a bias in REVEALS, as well as climate cooling may explain disparities between sites.

Main conclusions In the early and mid-Holocene, vegetation dynamics were probably more influenced by climate, as fire activity was low. During the late Holocene, fire activity and geomorphology, eventually augmented by human activities, increased in influence on vegetation dynamics and led to the predominance of the light taiga forest up to the present.

Keywords Charcoal, Disturbances, Palaeoenvironmental reconstruction, Pollen, REVEALS model, Russian boreal forest, Vegetation-fire interactions.

3.2. INTRODUCTION

Global warming calls for a better understanding of ecosystem responses to climate and human forcing (Spittlehouse and Stewart, 2003). In the higher latitudes, which are reacting fastest, climate change has been markedly affecting the vegetation dynamics and fire activity in the boreal region (Drobyshev et al., 2017).

Flannigan et al. (2009) consider that today's forest vegetation dynamics in boreal regions are controlled by both the fire regime and climate change. Johnson (1992) and de Groot et al. (2013) relate the fire regime to be influenced by the climate (for ignition) and vegetation (for fuel), and more recently by human activities. Furthermore, the climate, fire and vegetation are linked by complex interactions at different temporal and spatial scales (Higuera et al., 2009). At the regional scale, climate is considered as the main driver of Holocene fire regime and vegetation, while at the local level, topographic and vegetation factors could interfere with climate forcing (Hellberg et al., 2004). Studies of past fire activity, vegetation and climate dynamics, based on peatland or lake sediments, can document boreal forest dynamics at the ecosystem level or at the regional level of plant biogeography, and provide a better interpretation of the ecological mechanisms that govern their functioning (Petee, 2000; Botkin et al., 2007).

In Eurasia, two main types of boreal forests, called taiga, are present (Syrjänen et al., 1994; Shvidenko and Nilsson, 2000; Vygodskaya et al., 2007; Pflugmacher et al., 2011). They are defined by the presence of some predominant species and by an associated fire regime. This is light taiga when *Pinus sylvestris*, *Larix* sp. and *Betula* spp. are mainly present. A high frequency but low intensity fire regime (mainly surface fires) is associated with this vegetation-type (Lapenis et al., 2005; Schulze et al., 2005; Shorohova et al., 2009; Goldammer, 2015). It is the dark taiga when *Picea* spp, *Abies sibirica* and *Pinus sibirica* are mainly represented. A high intensity (crown fires) but lower frequency fire regime is associated with this vegetation-type (Lapenis et al., 2005; Schulze et al., 2005; Shorohova et al., 2009).

Well documented past vegetation/fire-related studies of the boreal biome are available from Fennoscandia, North-Western Russia and North America (Seppä and Birks, 2002; Higuera et al., 2009; Girardin et al., 2013; Clear et al., 2014; Kuosmanen et al., 2014; Stivrins et al., 2019). In these regions, boreal biome is largely dominated by *Picea*, *Pinus*, *Betula* and *Populus* species (Goldammer, 2015) and fires activity is generally associated with crown fires. In the Urals region of Russia, the links between fire, climate and vegetation during the Holocene are not

investigated as studies mainly focus on climate and vegetation dynamics (Antipina et al., 2014; Panova and Antipina, 2016). West of Ural, in the Komi Republic, two successive studies have documented the vegetation and climate dynamics based on pollen analysis of several sites (Baika, Kalya, Cherny Yar and Syndorsky, Figure III.1) during the Holocene (Sidorchuk et al., 2001; Golubeva, 2008). They showed that during the beginning of the Holocene (about 11,700 to 10,500 cal. yr BP), a light taiga composed of Scots pines (*Pinus sylvestris*), birches and spruces settled. At the same time, tundra disappeared, which was indicated by the disappearance of characteristic species of the tundra, such as *Artemisia absinthium* (wormwood), cereals and herbs (Golubeva, 2008). Subsequently, from 10,500 to 8800 cal. yr BP, the light taiga remained. *Abies* sp. appeared in the regional vegetation for the first time (Nikiforova, 1979). Then, from 8800 to 5300 cal. yr BP, pines and larches successively dominated the light taiga with the presence of spruces. A cool climate was associated with the disappearance of hardwood species. During the mid-late Holocene, from 5300 to 2500 cal. yr BP, birch development and spruce forests decreased, with fir trees reaching their maximum expansion between 4800 and 3400 cal. yr BP (Nikiforova, 1979; Golubeva, 2008). The gradual decline of spruce forests reinforced the light taiga which continued to strengthen at the end of the Holocene (from 2500 cal. yr BP to today; Golubeva, 2008).

Surface fires are currently the most common ecological disturbance for boreal forests of Eurasia. They are frequent, low in intensity, frequent and usually burn only part of the litter (Goldammer and Furyaev, 1996; Schulze et al., 2005; Goldammer, 2015). This fire regime is clearly associated with the boreal forests, especially the light taiga, which is composed of fire tolerant species such as *Pinus sylvestris*, and *Larix* spp. (Goldammer and Furyaev, 1996; Schulze et al., 2005). *Pinus sylvestris* for example, is a species that predominates on dry and sandy soils, and is well-adapted to surface fire regimes, with rather high frequencies (Fire Return Interval (FRI) of up to 20 years) (Goldammer and Furyaev, 1996; Drobyshev et al., 2004a). Indeed, fires induce pines to release their seeds and stands of trees are generally not damaged as they practice self-pruning of lower limbs, thus preventing fires from spreading up to the canopy, as well as having a thick, protective bark like *Larix* spp. (Sannikov and Goldammer, 1996). *Betula* spp. are also frequently found in light taiga because they are pioneer species that grow quickly after fires, simultaneously with *Pinus sylvestris*, but with faster growth (Schulze et al., 2005). In the boreal forests of Russia, dark taiga forest systems develop in association with a much lower fire frequency (Fire Return Interval around 200 years) (Goldammer and Furyaev, 1996; Schulze et al., 2005). These forests grow in wetter conditions

than light taiga and include *Pinus sibirica*, *Abies sibirica*, *Picea abies* and *Picea obovata* (Goldammer and Furyaev, 1996; Schulze et al., 2005; Tchebakova et al., 2009). In Komi Republic, most studies report the presence of *Picea obovata* (Drobyshev et al., 2004b, 2004a; Lopatin, 2007), but there are also studies reporting *Picea abies* (Kuuluvainen et al., 1998). There is no known bibliography citing the presence of either species. In the rest of the study, we will therefore use *Picea* spp. to characterise the spruce component of the vegetation.

As today's definition of boreal ecosystems rather strongly connect vegetation composition and fire type, it is interesting to transpose it into the past from which is inherited and anthropized today's pattern. In this paper, a paleoecological approach has been used to investigate the links between vegetation, fire and climate during the Holocene in the Komi Republic (in the western foothills of the Northern Ural region, Figure III.1). The fire history is revisited here from a charcoal analysis combining 4 cores from two peatlands in Yaksha area and validated by dendrochronological investigation of fire scars (Barhoumi et al., 2019). Palynological investigation carried out of the same two peatlands provides a continuous and medium-resolution record of the local vegetation dynamics. Instead of straightly comparing pollen assemblages and the fire regime, pollen signal is corrected of taphonomical biases using the LRA (Landscape Reconstruction Algorithm) approach (Sugita, 2007a, 2007b; Sugita et al., 2010; Hultberg et al., 2015) through REVEALS model (Regional Estimates of Vegetation Abundance from Large Sites). This consists in estimating quantitatively the regional vegetation (10^6 - 10^7 ha) from pollen records (Hellman et al., 2008). Here, five other pollen data are added. This regional reconstruction of vegetation dynamics (composition and structure along time) will help discussing long-term fire control over vegetation composition in Komi Republic and to compare with other boreal regions. It is hypothesized that during the Holocene, the dark taiga (i.e. forest dominated by *Pinus sibirica*, *Abies* sp. and *Picea* spp.) was associated with low fire frequency (FRI>200 years), while the light taiga was associated with high fire frequency (FRI<200 years). As the use of REVEALS models has never been tested in Russia we discuss the validity of the obtained taxa estimates before investigating taxon biogeography, in particular *Abies* and *Picea*, along distribution history.

3.3. MATERIALS AND METHODS

3.3.1. The study area

The Komi Republic is a Russian administrative division of 415 900 km², located on the western side of the Ural Mountains (Figure III.1a, Figure III.1b). The soils of the region are mainly moraine and surfaced loams (Zaboeva, 1997; Drobyshev et al., 2004), with podzolic soils and the topography is flat except near the Ural Mountains (Naryshkin, 2003). Currently, the population of the Komi Republic is about 1.12 million habitants.

In the north, the mean annual temperature is -6°C, while in the south, it is +1°C. The annual precipitation varies between 450 and 700 mm (Drobyshev et al., 2004a; Golubeva, 2008). The forest cover consists mainly of spruce (*Picea* spp., from 56% regionally in the Komi Republic to 13% locally in Yaksha, within a radius of 10 km, based on the resolution of Figure 1c), Scots pine (*Pinus sylvestris*, from 25% regionally to 84% locally) and birch (*Betula pendula* and *Betula pubescens*, from 1.4% regionally to 2% locally) (Figure III.1). Geographical scales therefore opposed the short prevalence of the dark taiga at a regional scale and a clear dominance of a light taiga locally. Ecologically, the young birch trees (Figure III.1c, Figure III.1d) follow the hydrographic network, as does *Picea* spp., which favors proximity to small rivers and marshy areas. *Pinus sibirica* and *Abies sibirica* may also occur near wetter areas.

The study sites are peatlands named Yak2 and Yak3 from Yaksha area (Figure III.1d) (Barhoumi et al., 2019). Two cores were extracted using an 8-cm diameter Russian peat corer from the center of the *Sphagnum* peatlands, and are named accordingly Yak2-A (168.5 cm) and Yak3-A (350 cm) (Figure III.1c, III.1d). Dominating tree species observed were *Pinus sylvestris*, and *Betula* spp. *Picea* spp. stands could be seen while crossing rivers and streams to access the two peatlands.

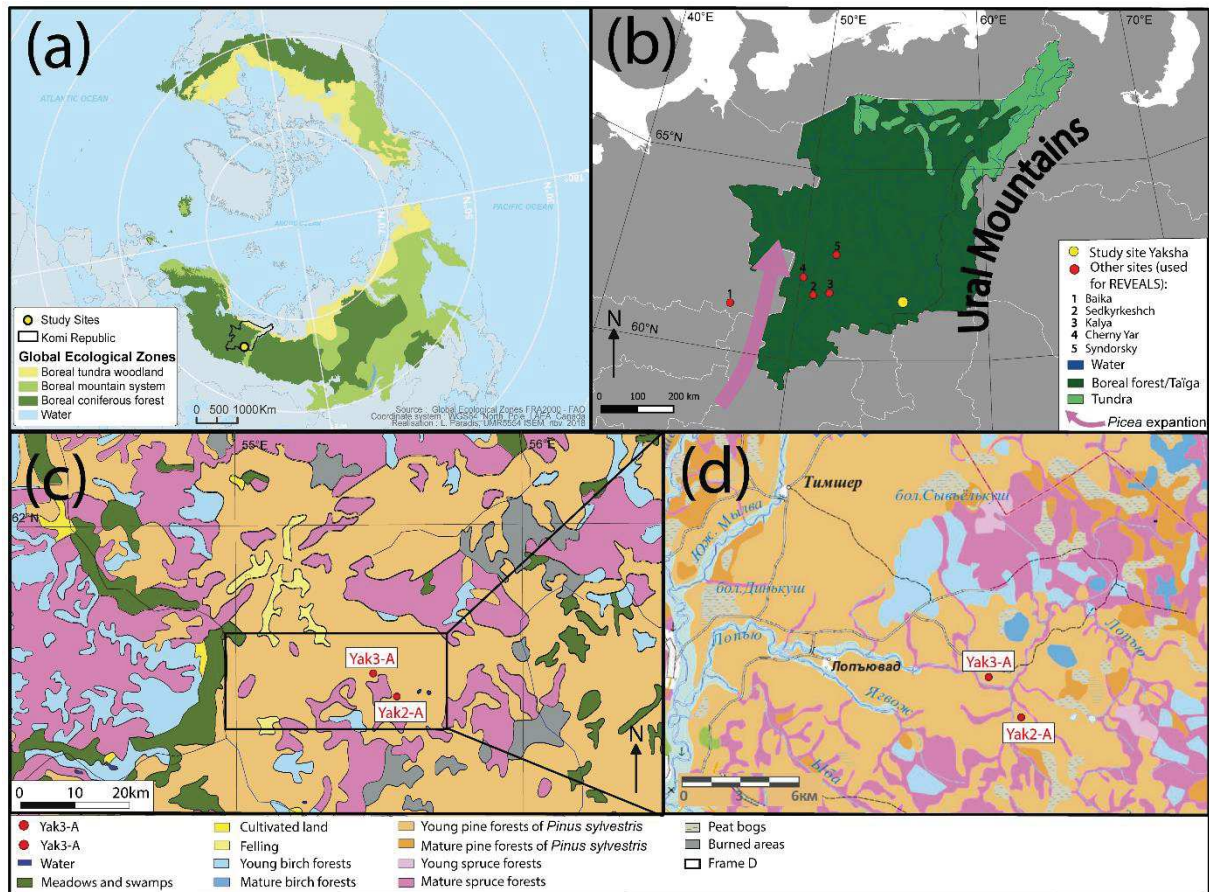


Figure III.1: Map of the study sites. (a): Location of the Komi Republic. (b): The Komi Republic and the assumed expansion routes of *Picea* spp. (c): Vegetation map of the study area. (d): Magnification of the study area at a finer resolution from the website

3.3.2. Dating and chronology of the peat cores

The chronology was based on five radiocarbon measurements from core Yak2-A, and seven radiocarbon measurements from core Yak3-A and discussed in detail by Barhoumi et al., (2019) (see Appendix S1, S4 and S5 and Figure III.2).

3.3.3. Pollen analysis

In the laboratory, the peat sequences were divided into 0.5-cm slices. In order to compare pollen and charcoal signals, so to cover the maximum time, a composite sequence was built from core Yak3-A and Yak2-A. In core Yak3-A, the 0 to 300 cm interval is offering the

best temporal resolution and his very top was preserved (contrary to Yak2-A). Samples were taken every 6 to 10 cm. The bottom sandy part was void of pollen. Lower part of core Yak2-A offered access to older time interval recorded in organic sediment, although with a lower temporal resolution. Samples were taken every 3 cm. Control samples were taken every 25 cm for the first 100 cm (overlap with core Yak2-A). A 3-cm³ subsample of sediment from the center of each slice underwent chemical treatment (HCl, KOH, HF, acetolysis) and 500 µm sieving (Moore et al., 1991). In core Yak2-A, 20 samples were counted and 4 were sterile (no pollen grains preserved, 219-year resolution). In core Yak3-A, 60 samples were counted and 18 were sterile (133-year resolution). The pollen analysis was carried out with a light microscope at a standard magnification of 400x. 39 pollen types were identified using the reference collection at ISEM and photo atlases (e.g. Reille, 1992, 1998; Beug, 2004). The two *Pinus* species (i.e. *sibirica* and *sylvestris*) were identified while *Betula* spp. (*pendula* and *pubescens*) and *Picea* (*abies* and *obovata*) subspecies were not distinguished. A minimum of 300 pollen grains was counted per sample, and the average sum was 315 pollen grains. Terrestrial pollen percentages were calculated based on the total terrestrial pollen sum, wetland taxa percentages were calculated based on the total wetland taxa (*Sphagnum*, Cyperaceae, *Typha/Sparganium* and *Menyanthes*). Pollen diagram plotting and local pollen assemblage zones were defined using the CONISS function of Psimpoll program (Bennett, 1992).

3.3.4. Application of the REVEALS model

To quantify the regional vegetation covers in the study area, the REVEALS model was applied (Sugita, 2007a). The parameters required for the REVEALS model are the radius of the basin, the pollen productivity estimates and the rate of fall of the pollen grains (PPE). As these parameters are not available for the region of Komi Republic, the PPE values were obtained from study conducted in Estonia (Poska et al., 2011) as this is the closest available dataset from similar bio-climatic region as the study area. This selection was based on the comparison of metadata of all modern pollen sites using PPE and the bio-climatic world map displayed in QGIS software (Sayre et al., 2014). The REVEALS model tends to correct the regional signal of large area record sites (Sugita, 2007a) and therefore, following Cao et al. (2018), the Yaksha vegetation signal was compared with other signals within a 500 km diameter around the site. Five previously analyzed pollen sequences were used from south to north, with the design of a new age-depth model when necessary (Appendix S6): Baika (Borisova, 2002), Sedkyrkesch

(Golubeva, 2008), Kalya (Karmanov et al., 2011a), Cherny Yar (Marchenko-Vagapova and Marieva, 2001) and Syndorsky (Golubeva, 2008) (Figure III.1b, Tableau III.1). The six pollen sequences were then homogenized in 23 time-windows from -50 to 10,500 cal. yr BP. The time-spans selected to record general vegetation patterns by REVEALS varied from 100, 150 and 400 years long for the 3 first time-windows to 500 years long for the others 20. The most recent time window was calculated only on the Yaksha values because the other cores do not cover the -50-50 cal. yr BP period (Tableau III.1). For the regional vegetation cover inferred from the REVEALS model (Figure III.5), the time-windows were set to 200 years and the diagram plotted with the Rioja package from R software (Juggins, 2009). The calculations were performed using the REVEALS 5.0 software and Prentice's model (1985) by means of the following parameters: $3\text{m}\cdot\text{s}^{-1}$ wind speed, and each lake radius (Tableau III.1). The results were plotted with the Psimpoll software (Bennett, 2008) and stratigraphically constrained cluster analysed with its CONISS function.

Tableau III.1: Pollen record information for the REVEALS model

Name of the site	Coordinates	Time covered (cal. yr BP)	Lake/peat radius (m)	References
Yaksha	61°43'N, 55°29'E 61°41'N, 55°34'E	-50 10,047	– 265	This study
Baika	61°16'N, 46°44'E	50 - 8775	365	(Borisova, 2002)
Cherny Yar	62°13N, 50°17'E	2876 - 8532	300	(Marchenko-Vagapova and Marieva, 2001)
Kalya	61°48'N, 51°47'E	0 - 10150	300	Karmanov et al., 2011
Sedkyrkeshch	61°43'N, 50°51'E	1197 – 4244	700	Golubeva, 2008

Syndorsky 62°44'N, 4727 - 9434 10900 Golubeva, 2008
51°51'E

3.3.5. Fire analysis

Sediment treatment and charcoal analysis were carried out by Barhoumi et al. (2019), following the conventional procedures recommended notably by Carcaillet et al., (2001) (see Appendix S1). The statistical treatment, and the calculation of compute and temporally smoothed mean Fire Return Interval (mFRI) is based on the four sedimentary cores of the Yaksha study site (see Appendix S1) (Higuera et al., 2009, 2011; Mudelsee et al., 2004; Barhoumi et al., 2019). A regime shift analysis was performed using the “change point” package (Killick and Eckley, 2014; Killick et al., 2016) with the R program (Team, 2014). The regime shift detection algorithm was used to identify periods of stable mFRI, from R-1 to R-5 (Rodionov, 2004; Rodionov and Overland, 2005; Drobyshev et al., 2016). A significance level of 0.05 was used for all the analyses, and to control for the weights of outliers, the Huber’s weight parameter was 2. A cut-off length of 4000 years was chosen for the evaluated regime.

3.4. RESULTS

3.4.1. Age models

Based on the two age models (Figure III.2), the Yak2-A core covers almost the entire Holocene period, from 11015 to -58 cal. yr BP, with a mean temporal resolution (deposition time) of 65.7 yr.cm⁻¹ (standard deviation = 29.3 years). Yak3-A is shorter than Yak2-A: it covers the mid-Holocene to the present day (6632 cal. yr BP to 53 cal. yr BP, lack of nearly the last 100 years) with a mean temporal resolution of 19.1 yr.cm⁻¹ (standard deviation = 9.9 years) (Barhoumi et al., 2019).

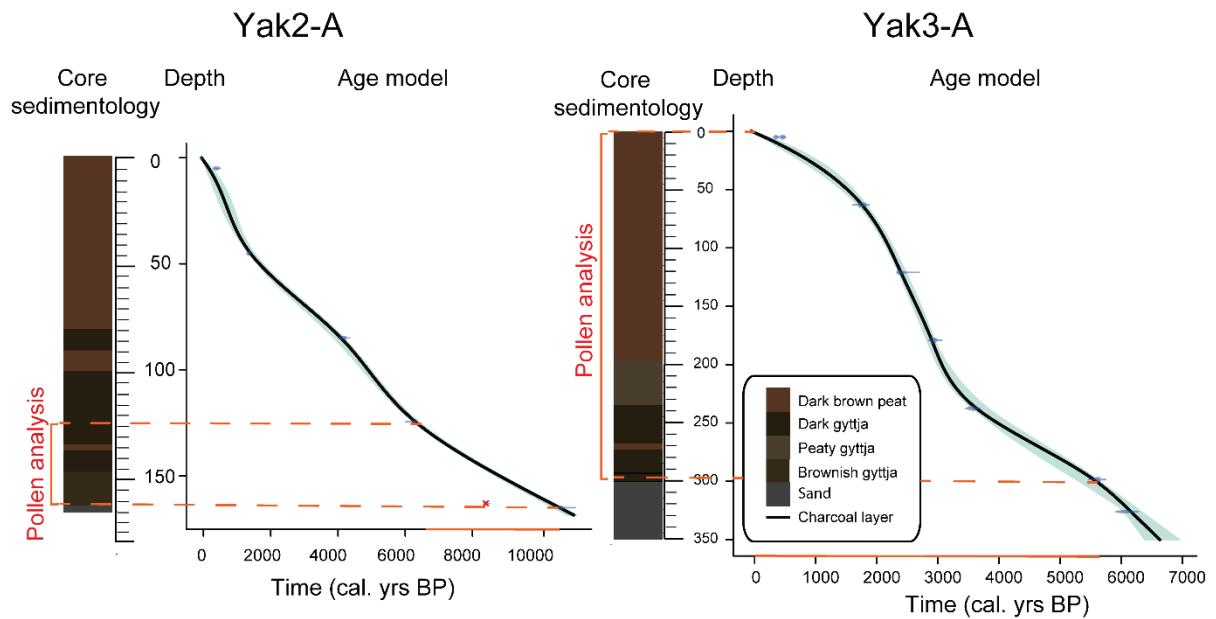


Figure III.2: Lithology and age-depth model based on calibrated radiocarbon ages, modified from Barhoumi et al. (2019). Red star is the age rejected by the age-depth model. The dashed and full orange lines indicate the part of the age model that was used in the pollen analyses.

3.4.2. Pollen and fire analyses at Yaksha

Analysis of the fire activity showed a gradual decrease in FRI during the Holocene, which translates into an increase in fire activity for the entire Yaksha study site (Barhoumi et al., 2019).

Composite sequence for pollen data was analyzed from Yak2-A for the early Holocene and subsequently from Yak3-A for the mid- and late Holocene. Terrestrial pollen assemblages from Yaksha (Figure III.3) were divided into 4 pollen zones labeled Z'1, Z'2A, Z'2B and Z'3 (Figure III.3). The pollen diagram indicates a forested landscape during the last 10,000 years. From 10 000 cal. yr BP to 6050 cal. yr BP (Z'-1 in Figure III.3 which corresponds to zone Z-1, see Appendix S2), the vegetation was dominated by *Pinus sylvestris* and *Betula*. These two taxa opposed: when *Pinus sylvestris* decreases, *Betula* increases ($r^2 = 0.81$). *Picea* was also recorded and showed close trends as *Pinus sylvestris*, while *Abies* and *Pinus sibirica* were absent during this period. Therefore, this period ranked today's description of a light taiga system. *Sphagnum* spp. related to the peatland itself where it developed on peat surface and wet soils. The percentage of wetland taxa Cyperaceae, temporarily increases between 9000 and 7800 cal. yrs

BP. This coincides with the R-1 and R-2 windows of the mFRI, and therefore indicates two distinct fire regimes: the first from 10,000 cal. yr BP to 7500 cal. yr BP with a median mFRI of about 400 years, and the second from 7500 to about 5800 cal. yr BP, with a median mFRI of 250 years (Figure III.3).

The zone Z'-2 extends from 6050 BP to 100 cal. yr BP and was characterized by an increase of *Picea* and the appearance of *Pinus sibirica*. It was divided into two subparts, Z'-2A from 6050 to 3200 cal. yr BP and Z'-2B from 3200 to 100 cal. yr BP. *Pinus sylvestris* and *Betula* showed different patterns and their relationship was more complex. *Pinus sibirica* appeared in Z'-2A and *Abies* in Z'-2B, signaling the establishment of a dark taiga forest. An increase of Cyperaceae at the beginning and the end of Z'-2A occurred, and during this period, the mFRI was 200 years (R-3). From 3200 to 100 cal. yr BP (Z'-2-B), the dark taiga decreased slowly and the light taiga reappeared, with the increase of *Pinus sylvestris*. At the same time, the median mFRI fell below 200 years (R-4, 135 years). More recently, there was a strong increase in *Betula*, which reached percentages above 65% (Z'3, from 100 cal. yr BP to 0 cal. yr BP), with the mFRI being less than 100 years (R-5).

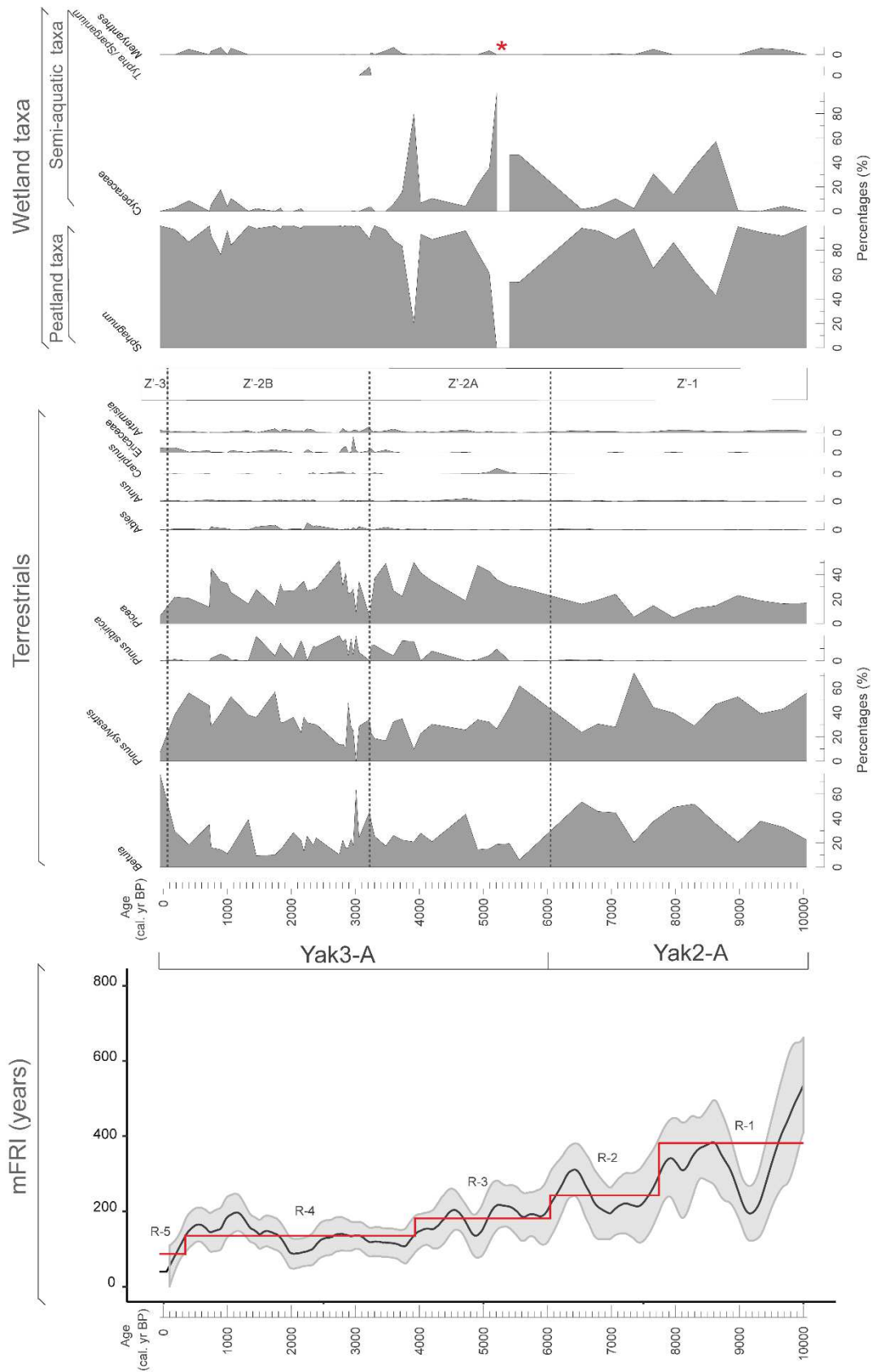


Figure III.3 : Pollen diagram versus age showing percentages of the main pollen taxa from the Yak2-A and Yak3-A cores, and the mFRI with the Rodionov regime shift zones, modified from

Barhoumi et al. (2019). The sample marked with a red star did not contain any Wetland taxa. The pollen diagram was divided into four zones with CONISS: Z'-1 from 10,047 to 6050 cal. yr BP, Z'2-A from 6050 to 3200 cal. yr BP, Z'2-B from 3200 to 60 cal. yr BP and Z'3 from 60 to -58.

3.4.3. REVEALS signals: Yaksha Vegetation Cover vs. Komi Vegetation Cover

REVEALS vegetation cover was divided using CONISS into 6 zones labeled M-1, M-2, M-3, M-4, M-5 and M-6. In general, the vegetation cover trends at Yaksha were similar to those observed at the regional level in the Komi Republic (Figure III.4). The notable differences were the grasses (Poaceae), which were not much developed in Yaksha (M-1, M-5 and M-6) and the regional development of *Abies* during the first half of the Holocene (M-2).

The trends of *Betula*, *Picea* and *Pinus sibirica* at Yaksha were similar to that observed at regional scale (the Komi Republic). For *Betula*, the only notable difference was at 5500 cal. yr BP (M-3), when it was less present (<5%) in Yaksha, compared to the regional signal (20%). For *Picea*, there was few differences in zone M-2, i.e. between 8500 and 8000 cal. yr BP, when it was much more represented in Yaksha (30%) than at the regional level (10%) and between 6500 and 6000 cal. yr BP, when it was less represented in Yaksha (30%) than at the regional level (60%). For *Pinus sylvestris*, during the first half of the Holocene (M-1, M-2 and M-3), this taxon was more locally represented in Yaksha (generally >10-15%) than at the regional level. The signals between the pollen results and REVEALS reached similar levels at 5000 cal. yr BP (M-3). Finally, *Abies* was the taxon that showed the most differences between the two signals. At the regional level, *Abies* strongly developed from 8500 cal. yr BP (about 40%, M-2), then gradually decreased to less than 10% at 6500 cal. yr BP (M-2). In contrast, at Yaksha, its signal was constant but much lower during this period (around 10%). Subsequently, after 6500 cal. yr BP, the two signals showed more consistency (M-3, M-4 and M-5). Thus, it is more likely that *Abies* developed in Yaksha at the time of its second wave in the Komi Republic, from 5000 cal. yr BP (M-3), when the two signals could be corroborated. *Alnus* and Poaceae taxa were poorly represented in the Yaksha site. With the REVEALS model, *Alnus* remained relatively low in the regional representation (maximum 3%, in M-3, around 4500 cal. yr BP). For Poaceae, high percentages were reconstructed at the beginning of the Holocene in zone M-

1, between 10,500 and 10,000 cal. yr BP (30%), though their presence decreased strongly thereafter and remained below 3%, before gradually increasing from 1000 cal. yr BP, to reach about 8% at 50 cal. yr BP (M-5 and M-6). The dynamics at the regional level were not the same as at the local level in Yaksha, since the presence of Poaceae was only slightly visible between 5500 and 5000 cal. yr BP (2%, M-3). In contrast, *Artemisia* percentages were similar at the local and regional spatial scale. Concerning *Pinus sibirica*, results between Yaksha and Komi regional signals were similar. Percentages were low at the beginning of the Holocene from 10 500 until 4000 cal. yr BP, and then the signal increased in M-4, reaching about 5% at 2500 cal. yr BP, after which it decreased again to values close to 0% in the M-6 zone.

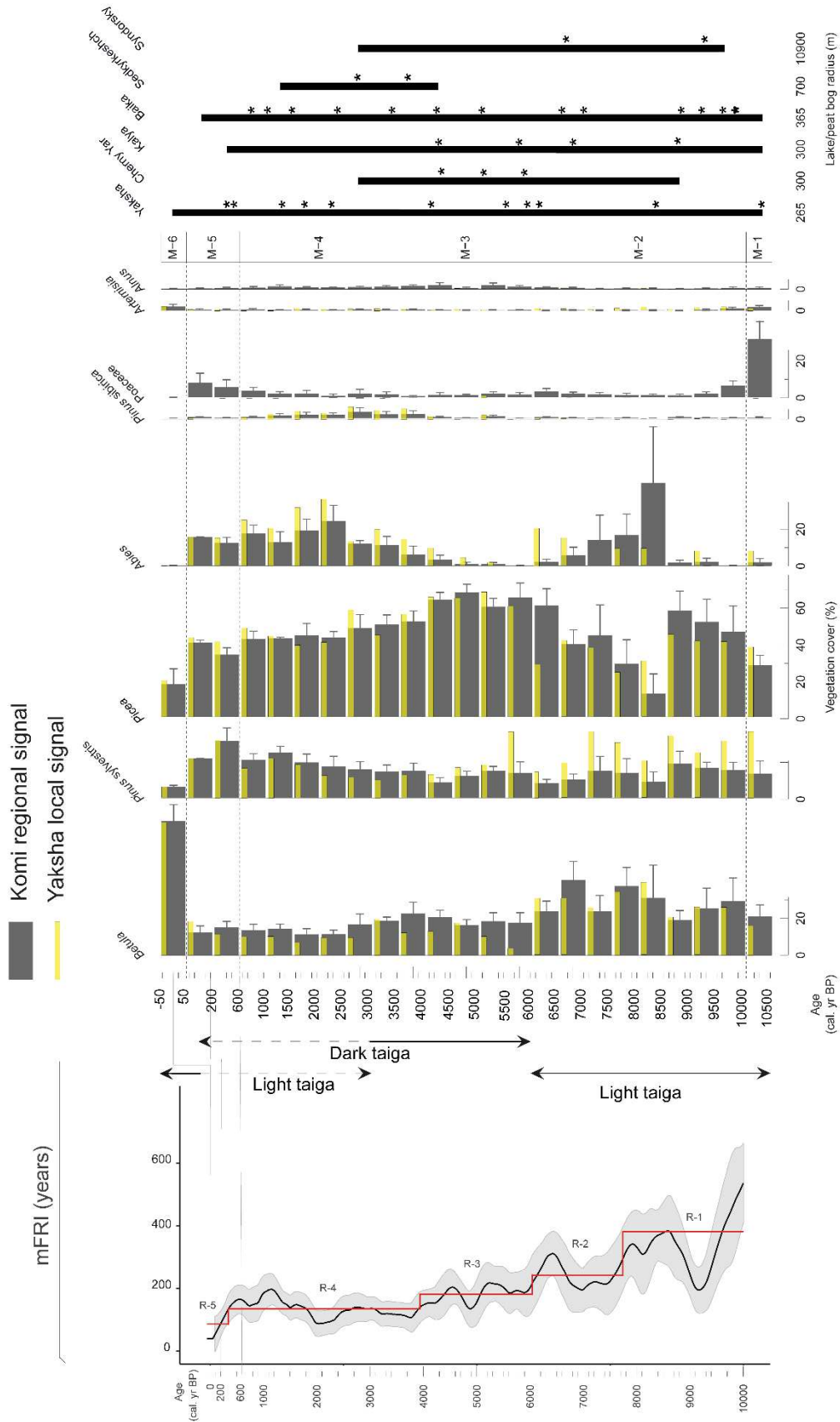


Figure III.4 : Vegetation diagram versus age inferred from the REVEALS model showing percentages of the main forest taxa at the Yaksha site, compared to vegetation at the regional scale. In the histogram, an error bar (± 1 standard deviation) is represented for each estimate made by REVEALS. The contribution of each site to the reconstruction of REVEALS is represented on the left by a bar that indicates the time window over which the site data extends. The radius corresponds to the size of lakes or peat bogs. The black stars to the right of each site correspond to the radiocarbon dates (median cal. yr BP). The mFRI with the Rodionov regime shift zones are represented, modified from Barhoumi et al. (2019).

3.5 DISCUSSION

3.5.1. Holocene vegetation dynamic, fire activity and climate

3.5.1.1. Republic of Komi

The relatively low fire activity from 10 000 to 6000 cal. yr BP is associated with light taiga. Increase of *Picea* at 9000 cal yr. BP lead to forest densification. This was most probably caused by more continental and climatic conditions that occurred from 9600 cal. yr BP with colder temperatures (-3.5°C to -2.5°C in January and -0.5°C in July) and rainfall higher than currently (850 mm per year) up to 9400 cal. yr BP (Sidorchuk et al., 2001; Golubeva, 2008). Around 8500 cal. yr BP, a warming of temperatures allowed the appearance of *Abies* (Golubeva, 2008). These two taxa were markers of dark taiga, which brings a nuance concerning the light taiga system present. During phases M-1 and M-2, the forest was mainly light taiga, but dark taiga marker species were still present. Dark taiga is sensitive to burning (Goldammer and Furyaev, 1996), but mFRI remained high (median R-2 at 250 years) and thus was compatible with the presence of *Picea* and *Abies*.

From 6000 to 3500 cal. yr BP (M-3), the dark taiga was at its maximum and development and compatible with reconstructed levels of fire activity with median mFRI at ca. 180 years (R-3) (Gromtsev, 2002; Schulze et al., 2005). Golubeva (2008) observed a warming up to 5300 cal. yr BP, followed by a cooling up to 5100 cal. yr BP. Sidorchuk et al. (2001) reported a slight increase in humidity at 700 mm per year around 5100 cal. yr BP, congruent with the dominance

of *Picea*. During this period, in the study area, the concomitant increase in Cyperaceae over *Sphagnum* recorded in Yaksha, may attest for a higher water table in wetlands, and therefore corroborates that the moisture factor may be more important than the influence of fires shaping the vegetation dynamics and composition.

From 3500 to 50 cal. yr BP, there was a decrease of the mFRI (at ca. 135 years; R-4), which may have been facilitated by the increase in summer temperatures (2 to 3°C more than today) at the beginning of this period (Golubeva, 2008, Klimanov's method). The decrease in mFRI could be the cause of a reappearance of the light taiga and the reduction of the dark taiga since such values of mFRI are incompatible with this kind of forest according to Goldammer and Furyaev (1996). From 600 to 50 cal. yr BP (M-5), the dominance of the light taiga was re-established, but dark taiga patches remained (presence of *Picea* and *Abies*). The fire activity was high and consistent with this type of forest, despite decreasing temperatures (Goldammer and Furyaev, 1996; Gromtsev, 2002; Hille and Den Ouden, 2004; Golubeva, 2008; de Groot et al., 2013). Indeed, *Pinus sylvestris* has highly flammable needle foliage, but is able to self-prune its lower branches, which reduces the possibility of tree death when a fire event occurs (Schulze et al., 2005). There was also a steady increase in Poaceae at a regional scale (100 cal. yr BP, M-5), which occurred when temperatures increased and rainfall gradually decreased to current values (around 700 mm per year) (Sidorchuk et al., 2001; Golubeva, 2008). This can indicate intensified anthropogenic use of the landscape generally going hand in hand with the decrease of FRI. Both elements can highlight the relationship between human activities and the increase in fire activity during this period. Furthermore, this is accompanied by temperatures increasing and rainfall gradually decreasing to current values (around 700 mm per year).

The phase M-6 (50 to -50 cal. yr BP) was characterized by a sharp increase in *Betula* spp., probably resulting from the increased human impact favoring fires. The climate was the same as it is today (Golubeva, 2008). Indeed, fire activity was the highest of the Holocene (mean mFRI = 81 years), with *Betula* spp. colonizing as a stand-replacing fire species (Schulze et al., 2005). Combined with greater human activities, such as cutting and clearing, these contribute to becoming the main sources of ignition and increasing the fire frequency (Naryshkin, 2003; Drobyshev et al., 2004a).

3.5.1.2. Boreal biome vegetation-fire interactions

One of the major issues in the functioning of boreal forests is to understand when fire controls vegetation and when climate has a greater impact and vice versa. The study of past FRI is an interesting tool to understand these mechanisms and identify key periods when fire is the determining factor in vegetation composition, especially when it reaches threshold values. In the North American boreal forests, various fire regime changes took place during the Holocene (Bergeron, 2000; Ali et al., 2008; Higuera et al., 2009; Carcaillet et al., 2011). Unlike the Yaksha study, northern Quebec forests (*Picea glauca*, *Abies balsamea*) have had an increasing FRI since 800 cal. yr BP (FRI of about 300 years nowadays), in part due to wetter climatic conditions and reduced sunlight (Carcaillet et al., 2011). Forests in southern Quebec (*Abies balsamea*, *Betula papyfera*), on the other hand, have had a decreasing FRI for about 2200 years with a current value of about 200 years, similarly to those in the Republic of Komi for the R-4 phase. In both cases, Carcaillet et al., (2011) determined that the change in FRI did not significantly affect the composition of the boreal forest, because on the one hand, a high vegetation diversity allowed resilience and on the other hand, the critical threshold values of FRI were not reached. This is the case in the Republic of Komi, during the R-4 phases.

In central Siberia, the forest is a dark taiga, with a dominance of *Picea* spp. /*Abies* sp. at the late stage of succession (Schulze et al., 2005). In this ecosystem, disturbances such as fire, wind throws and insects did not affect the nature of the successional stages that occur in this region. However, after a fire-type disturbance, the initial state is restored after about 400 years. Factors such as species ecology (growth/longevity/reproduction) play a major role in the regeneration of the species (Schulze et al., 2005). This can be compared with the R-3/M-3 phases of the study, where dark taiga persists, despite an increasing FRI but threshold not reached, indicating a higher fire activity.

Another study in northwest Russia showed that local conditions also play a major role in the composition of boreal forest vegetation (Kuosmanen et al., 2014). Thus, the parallel study of three sites (distances between sites from 800 m. to 70 km.) showed that in the same region, local conditions have an impact on the fire regime, which was not the same within the three sites. At Yaksha, the 3 study sites did not show the same local recent fire activities when tree ring fire scars were analyzed (Barhoumi et al., 2019). In the study of Kuosmanen et al., (2014), the different fire regimes were associated with different kind of vegetation dynamics. When fires were frequent, the diversity of species was greater and *Picea* spp. was not among the dominant species, while when fires were absent, *Picea* spp. became a dominant species. However, despite different fire histories, the three sites showed a common decline of *Picea* spp.

at the end of the Holocene, indicating a stronger impact of the regional climate (Kuusmanen et al., 2014).

3.5.2 Reflection on REVEALS method

The REVEALS method has been tested and validated by several studies of regional vegetation in Sweden, across the Holocene, and especially in the correction of the signal from species that produce few pollen, such as *Picea* sp., but also from species that produce a lot of pollen such as *Pinus* sp. and *Betula* spp. (Anderson et al., 2006; Hellman et al., 2008; Sugita et al., 2010). REVEALS has also been used to estimate vegetation cover in areas other than boreal forests, such as the Tibetan Plateau, for the Holocene period as well (Wang and Herzschuh, 2011). The use of pollen records from multiple small sites, as in this study, instead of the use of pollen records from large lake, was also tested in Sweden by Trondman et al. (2016). Their study showed that vegetation estimates were good with this kind of data but noted some failures, notably with the estimates of Cyperaceae and *Betula* spp., through the use of bog-type sites.

The data required for the proper use of REVEALS are the size of the lake/peat, the pollen records and the pollen productivity estimates (PPE). However, the PPE, which is related not only to the species, but also to the region where the species is established, is not accessible for all regions because it has not been estimated everywhere (von Stedingk et al., 2008; Bunting and Hjelle, 2010; Xu et al., 2014) is not yet developed in the Republic of Komi (Lisitsyna et al., 2017). Therefore, the selection of PPE from Estonia was chosen because this site has a forest similar to the one studied in the Republic of Komi and is situated at the same latitude (Poska et al., 2011). The climatic conditions are also not so different, unlike Sweden, where the vegetation is subject to climatic constraints very different from our study area (Broström et al., 2008; Poska et al., 2011). However, the PPE specific to Komi Republic species may be different from the one used and this should be kept in mind when interpreting the results.

Concerning the results of *Abies* sp., first increase of this taxa in M-1 and M-2 (Figure III.4) should be taken with caution, because records show too different pattern when looking at the details from Figure III.5b. In Yaksha, REVEALS model estimates >10 % of *Abies* forest cover from only 1 or 2 pollen grains per sample. This is also the case for the Kalya site, with only 2 grains of *Abies* sp. pollen counted at 6347 cal. yr BP, however for the Cherny Yar site, *Abies* sp. raised around 60% with 9 and 39 pollen counted during the early Holocene. Indeed, Poska et al. (2011) determined an average value of 6.71 that was used for REVEALS in this

investigation. Abraham et al. (2014) also observed unrealistic REVEALS estimates of *Abies* sp. cover in the Czech Republic and attribute them to regionally variable PPE of *Abies* sp. In addition, although *Abies* sp. pollen is heavy and does not transport easily, pollen may still be found in areas where the tree is not present, indicating that it can be transported by other means (Poska and Pidek, 2010). For example, in the high Plateaus of Armenia, where fir is not growing, few *Abies* pollen grains are regularly found throughout Holocene records (Joannin et al., 2014; Leroyer et al., 2016). The pollen transport that occurs in the Komi area must therefore be considered as another bias possible, which may affect vegetation estimates made with REVEALS. The Republic of Komi is close to the Ural Mountain Range, which does not necessarily prevent long-distance pollen transport (Frei, 1997; Rogers and Levetin, 1998; Smith et al., 2008), and several pollen studies have shown that in Northern European Russia, some taxa are over-represented both in relation to pollen production and in relation to long-distance transport (Paus, 2000). The most often over-represented taxa are *Betula* spp., *Pinus* sp. and *Alnus* sp. (Paus, 2000; Siljamo et al., 2008; Novenko et al., 2017) while the taxa that are likely to come from long-distance transport are *Picea* spp., and *Carpinus* sp (Latałowa and van der Knaap, 2006; Novenko et al., 2017). Fires themselves may have been a source of long-distance pollen transport by air convection (Pisaric, 2002). Therefore, *Abies* might be also added to the list of over-represented taxa by the mean of long-distance transported grain that the use of PPE from Estonia cannot correct in terms of cover estimates. For more caution, REVEALS results in sites Yaksha and Kalya should only be taken into account for the second *Abies* rising, which is consistent with the study conducted by Golubeva (2008), indicating the presence of fir trees for the first time from 5900 cal. yr BP,.

Dating error and number of dating for each site is an independent bias to consider in both pollen and REVEALS results interpretation. Concerning *Picea* spp. estimation from Figure III.5a, a *Picea*'s spp. acme was centered on around 8000 cal. yr BP in Baika, 7000 al. yr BP in Syndorsky, 5200 cal. yr BP at Yaksha, and around 5000 cal. yr BP in Kalya and Cherny Yar. The age model of Syndorsky, based only on two ¹⁴C dating, is a source of uncertainty regarding the dynamics of *Picea* spp. and without the Syndorsky site, a south to north expansion gradient (from Baika towards Cherny Yar) could have occurred. This does not correspond to the east-west gradient described by Giesecke and Bennett (2004), but since the Komi Republic is more continental than their study area, other expansion paths may have occurred. However, the data from the Syndorsky site do not allow for the validation of a clear spread from south to north in the Komi Republic.

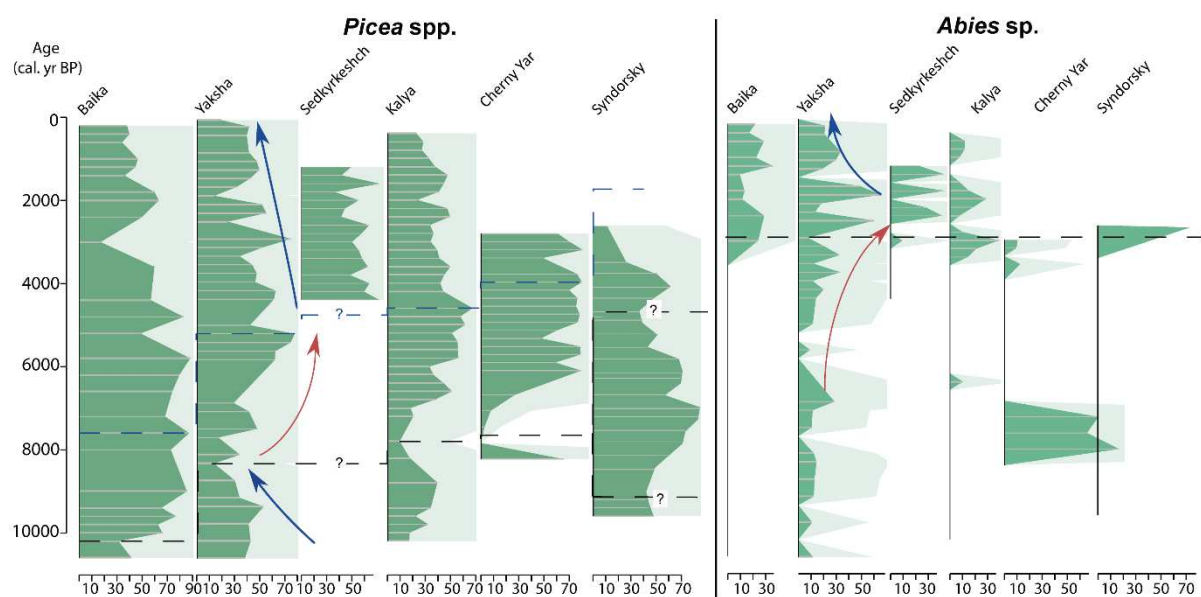


Figure III.5: Vegetation diagram versus age from the REVEALS model showing the evolution of *Picea* spp. and *Abies* sp. The sites are ordered according to a south-north gradient.

3.5.3. Ecology and Holocene plant biogeography of the Komi Republic

We have observed that fire activity, which is today the primary disturbance over vegetation in the boreal forest, was not triggering vegetation dynamics during the early and mid-Holocene. Long-term climate indeed appears as the major driver in shaping the landscape of the study area. This is particularly pregnant when assuming that, ecological processes like post-glacial migration and recolonization from refugial zones are slow for plants in general and for long-living trees in particular. According to Feurdean et al., (2013), *Picea* migration speed in this region is in the order of 60 to 260 m per year (60 to 260 km/1000 years). Therefore, linking species distribution and cover estimates against time site by site can help to understand taxon biogeography during the Holocene. Thus, time controls are essential in order to assert time lags interpretation. Among the main factors considered in paleoecology, one can cite soil characteristics, seedling and competitiveness (Birks and Birks, 2004; Rull, 2005). In the case of Boreal ecosystem, low diversity invites to individually select taxon features through time and to investigate spread, acme and decline, with all possible range expansion or contraction. We present this comparison for *Picea* and *Abies* in Figure III.5. We did not investigate *Pinus* taxa because species distinction between *P. sibirica* and *P. sylvestris* was done in Yaksha, but not in

the other sites. Similarly, *Betula* was not selected because it is a pioneer species, has a short life cycle and has colonized the region since the end of the Late Glacial (Sannikov and Goldammer, 1996).

3.5.3.1. Spruce biogeography

Picea spp. was recorded at all sites and was likely present all over the 10,500 yrs compared in this study. The Baika and Yaksha pollen records, further south, showed an early presence of this taxon at the beginning of the Holocene (10,500 cal. yr BP), as well as the Kalya site (10,000 cal. yr BP) (Figure III.5b). This is consistent with a Late Glacial *Picea* spread as reported in Fennoscandia by Giesecke and Bennett (2004) in their synthesis based on modeling of geographical expansion across the Holocene with pollen percentage thresholds. These authors reported that after an early and rapid Holocene spread, the northern populations remained low or even declined before 8000 cal. yr BP (Tolonen, 1983; Giesecke and Bennett, 2004), then they demonstrated a general spread with high population densities moving from east to west around 4000 cal. yr BP.

The first event observed in the Komi Republic is a drop of *Picea* spp. at 10,100 cal. yr BP in Baika, 8500 cal. yr BP in Yaksha, 8000 cal. yr BP in Kalya, and 7900 cal. yr BP in Cherny Yar (Figure III.5b). To explain the falls in their *Picea* spp. populations, Giesecke and Bennett (2004) listed several hypotheses, such as competition by birch, climate change and genetic diversity. These hypotheses can also be applied to the population in the Komi Republic. In our study area, REVEALS estimates indicate that *Betula* is increasing when *Picea* decreased. It is also the case with *Abies* (Figure III.4), which may indicate that competition has occurred between these taxa. The present study can more clearly state that the fire activity, not in the hypothesis list from Giesecke and Bennett (2004), was not in control of this spruce decline which occurred when the median mFRI was at ca. 350 years (R-1).

A study by Väiliranta et al. (2011), based on analyses of pollen, stomata and macrofossils in the Pechora region (including two sites in the north of the Komi Republic), supports the idea of several small local expansions of tree populations from different isolated patches rather than a broad-scale general movement. This could be one of the causes of the observed discrepancies between the dynamics of *Picea* spp. of the different sites.

Finally, the results of Tollefsrud et al., (2015) and Tsuda et al. (2016), based on pollen data and *Picea* spp. DNA, showed that the Urals region was an area of hybridization and introgression between the species *Picea abies*, from Fennoscandia and *Picea obovata*, from Siberia. The introgression (the precise period is not yet known) between these two species could have had an impact on the fitness of *Picea* spp. populations and also be a source of variability in terms of population dynamics in the Komi Republic.

3.5.3.2. Fir biogeography

The early presence of *Abies* sp. at the site Cherny Yar was not unique in the Komi Republic, because it was also reported in the region by Nikiforova (1979) since the first appearance of this taxon occurs between 10300 and 8800 cal. yr BP, with summer temperatures 1°C higher than today's from 10500 to 9600 cal. yr BP (Golubeva, 2008). Very high local soil moisture conditions or particularly low fire activity may be the reasons for a dynamics in favour of its development within this particular site improving its competitiveness against *Picea* spp. between 8500 to 7000 cal. yr BP (Furyaev et al., 1983).

Then the regional climatic conditions, such as annual temperatures cooling between 7400 and 6400 cal. yr BP could have prevailed over the local particularity of the Cherny Yar site and favoured the expansion of *Picea* spp. over *Abies* sp. from 7000 cal. yr BP (Golubeva, 2008; Seppä et al., 2009b), before a global expansion of *Abies* sp. in the Komi Republic around 3000 cal. yr BP observed in Baika, Yaksha, Sedkyrkesch and Kalya. This is consistent with the study conducted by Nikiforova (1979) about this species in the Komi Republic but occurred later than the maximum expansion observed by Golubeva (2008) between 5000 and 4800 cal. yr BP. However, for the Baika site, revisited age model and REVEALS results show a presence of *Abies* sp. earlier (from 3800 cal. yr BP) than the study of Sidorchuk et al. (2001) (around 1400 cal. yr BP).

The decline in *Abies* sp. generally observed around 2000 cal. yr BP was also described by Nikiforova (1979) when the annual climate temperature decreased by 2.5 to 3°C compared to current values and in addition to the increase of fire activity, it led to a deterioration in the species' growing conditions (Golubeva, 2008). Today in the Komi Republic, *Abies* sp. populations are limited to the Ural Mountains.

4.3.3 Ecosystem biogeography

Today, at Yaksha, *Picea* spp. are mainly found around peatlands themselves often distributed along the head of small streams, and thus on moist soils (Figure III.1d), while *Betula* spp. can be observed along eroded riversides (Figure III.1d). The first half of the Holocene showed a strong climatic influence on vegetation dynamics. The opposite trends of *Betula* spp./*Picea* spp. were therefore largely controlled by this factor during this period (Figure III.3 and Figure III.4). From 6000 cal. yr BP, the hydrographic and peat networks could have become more developed and extensive in Yaksha when the system filled in by organic and sediment accumulation as over the Holocene. *Sphagnum* peat replaced Cyperaceae mires (Figure III.3), thus the expansion of humid soils may also have favored the development of a dark taiga composed first by *Picea* spp. pure stands, and secondly by *Picea* spp. mixing with *Pinus sibirica* and *Abies* sp. Such hypothesis for the dynamics of soils and river systems was likewise suggested by Zaretskaya et al. (2014) to explain the chronology of geological events such as lake dynamics in the Vychegda River Valley of the Komi Republic. This dark taiga was likely limited spatially to low areas and stream systems, contrary to the light taiga that was found on slightly higher areas. Local distribution of light and dark taiga growing at the same period also supports the idea of several small local expansions of spruce populations suggested by Väiliranta et al. (2011). However, these expansions were not from different isolated patches but rather from ecological corridors distributed along the hydrographic system.

The mixed coniferous dark taiga was first controlled and then suppressed by the fire regime, which took control over climate in the ecology of Boreal forest in the late Holocene. This ecosystem has locally no more equivalent today as only spruce remains. The significant presence of *Betula* spp. found at late Holocene corresponded to the last sample from the site Yaksha (dated at -58 cal. yr BP). It does not match with the vegetation map (Figure III.1c and III.1d), but two reasons can explain that. The first is that the map was created before the age of the last Yaksha sample (CE 2008) and the second is that the area is now subject to logging as it is showed by Appendix S3 where we can see the logging of *Picea* spp. stands in CE 1984, and the fast recolonization of *Betula* spp. in CE 2016.

The local dynamics of the site Yaksha, provided by the pollen record have been highlighted, with regard to regional vegetation, through the use of REVEALS. The analysis of pollen and charcoal from the sequences Yak3-A and Yak2-A has allowed the landscape dynamics to be determined in the Yaksha area, in the Komi Republic during the Holocene, revealing the

complex patterns between the landscape morphology, and the plant species in relation to the climatic context and the nature and frequency of fires. At the beginning of the Holocene, the climatic context of the site was probably primordial for the establishment of the vegetation, until about 3500 cal. yr BP. After this period, increasing fire activity played a major role in the disappearance of the dark taiga, in favor of the light taiga. Currently, intense fire activity, partly due to human activities, is the dominant factor influencing the vegetation dynamics. Fire management efforts should be continued in this area, given the current climate change, which have caused the extreme fires that have been taking place in Siberia in the summers in recent years, but which could also take place in the study region.

3.6 ACKNOWLEDGEMENTS

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3.7 BIOSKETCH

Chéïma Barhoumi is currently working as a PhD student at the Institut des Sciences de l'Évolution Montpellier (ISEM) at the University of Montpellier in the Dynamics of Ecosystems and Global Change team (<http://www.isem.univ-montp2.fr/fr/equipes/dynamique-des-ecosystemes-et-changements-globaux-index/>). Chéïma does research in paleoecology. His thesis topic is the history of fires, vegetation dynamics and climate variability in the boreal forests of Russia (Komi Republic) during the Holocene.

3.8 APPENDICES

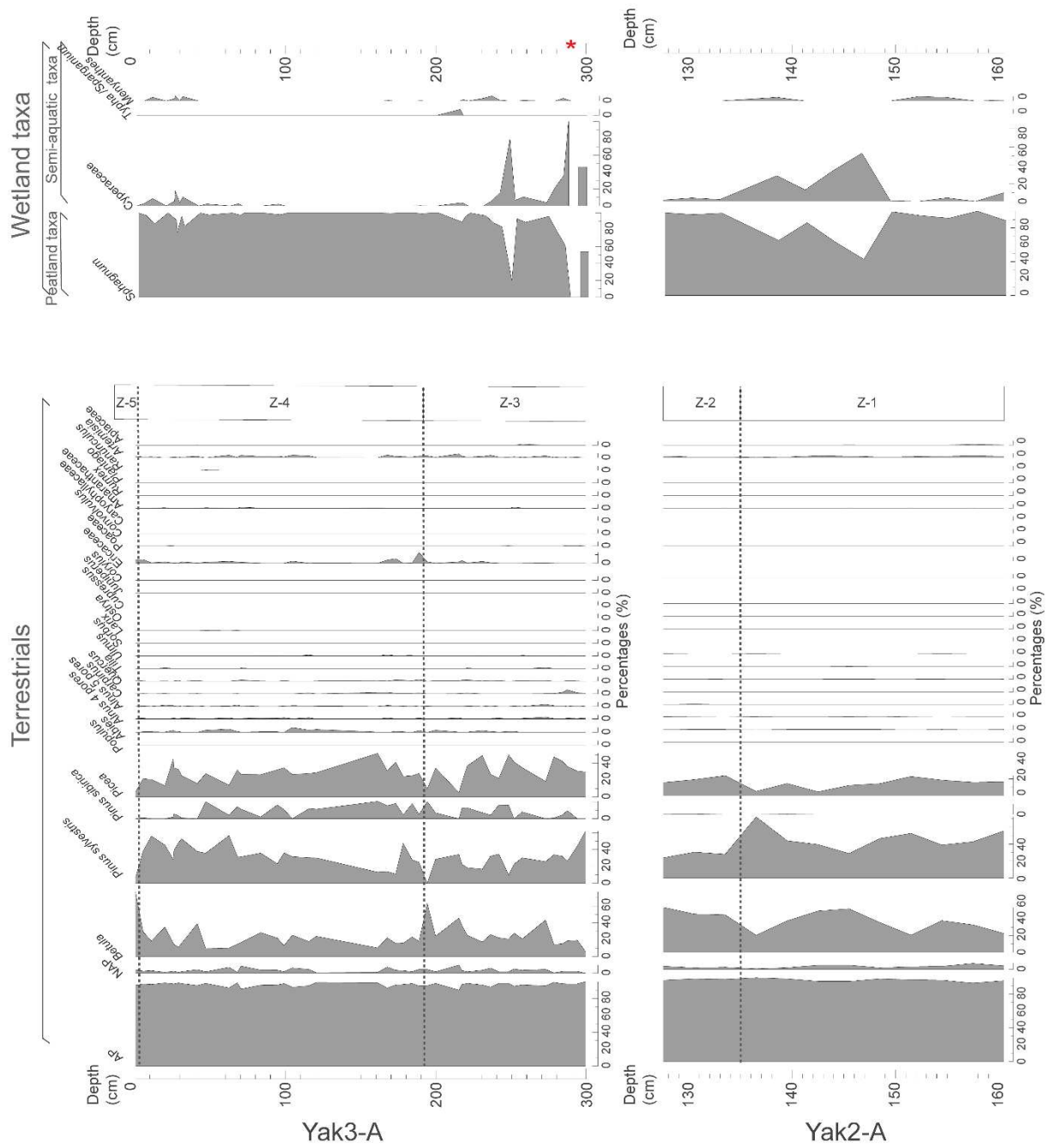
Appendix S1:

Dating and chronology of the peat cores Samples for dating were obtained from charcoal, plant macro-remains and bulk sediments. The radiocarbon dates were calibrated using the R package CLAM 2.2 (Blaauw, 2010), IntCal13 provided the calibration curve (Reimer et al., 2013), while the NH1 post-bomb calibration curve was employed for the modern radiocarbon (Hua et al., 2013). A smooth spline function at 0.28 degrees was used to fit the age models (Blaauw, 2010) with a 0.95 confidence interval.

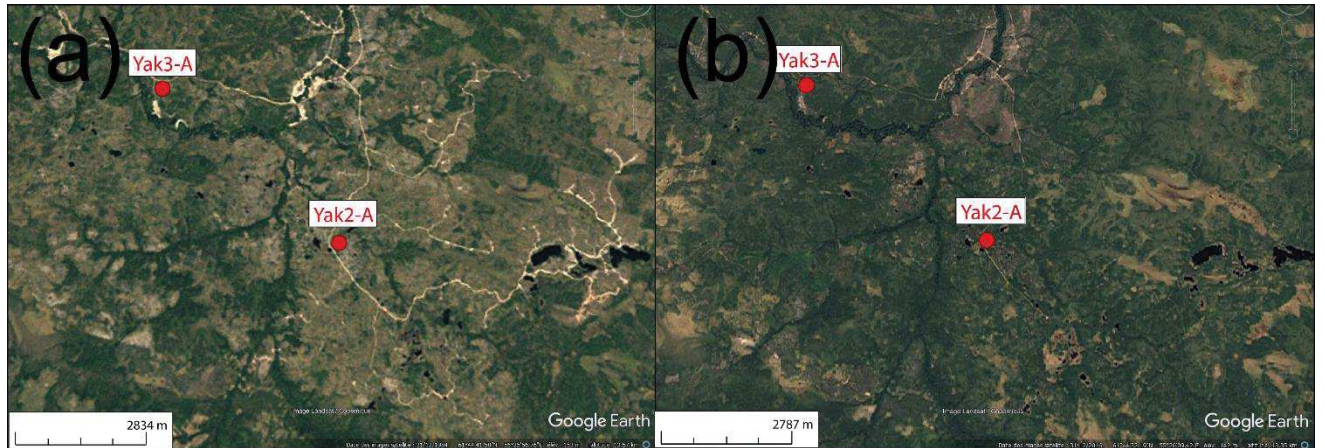
Fire analysis detailed method Peat sequences were cut into 0.5 cm slices. 1-cm³ subsamples were taken from each slice and were treated following a standard protocol (Carcaillet et al., 2001). After 160 µm sieving, charcoal particles were counted and measured under the microscope with the WinSEEDLE software (Regent Instruments Canada Inc, 2009). Fire events were identified using the program CharAnalysis (Higuera et al., 2009, 2011). The CHAR series comprise low-frequency (background; $C_{\text{background}}$) and peak (or residual series; C_{peak}) components. $C_{\text{background}}$ was estimated with a robust Lowess using a 300–500 year window width (Brossier et al., 2014). C_{peak} values were obtained by subtracting $C_{\text{background}}$ from $C_{\text{interpolated}}$, which corresponded with a resampled record of the CHAR series. The C_{peak} series were then divided into two sub-populations: (i) noise, which represented variability in sediment mixing, sampling and the noise induced by numerical analyses; and (ii) fire events (C_{fire}), representing fires occurring 1–10 km from the peat core sites. For each sample, a Gaussian mixture model was used to identify the noise distribution, with a 99th percentile threshold for separating samples into fire and non-fire events (Higuera et al., 2007). The fire-return interval (hereafter FRI) values, corresponding to the time between two consecutive fire events, were obtained from the raw C_{fire} series. A Kernel density function (Mudelsee et al., 2004) was used to compute a temporally smoothed FRI. The software *tauest* (Mudelsee, 2002), *kernel* (Gasser and Müller, 1979, 1984) and *redfit* (Schulz and Mudelsee, 2002) were also employed. The mean FRI (mFRI) was determined on the basis of pooled FRI for all peat sequences, and the 90% confidence intervals were calculated from the distribution of the 1000 resampled FRI series, and are presented for a 300-year bandwidth.

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Appendix S2: Pollen diagram versus depth showing percentages of the main pollen taxa of the Yak2-A and Yak3-A cores. Only the depths studied are represented. In the Yak 3-A core, the sample marked with a red line and a red star did not contain any Wetland taxa.

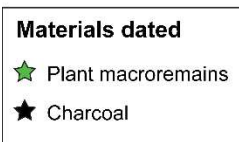
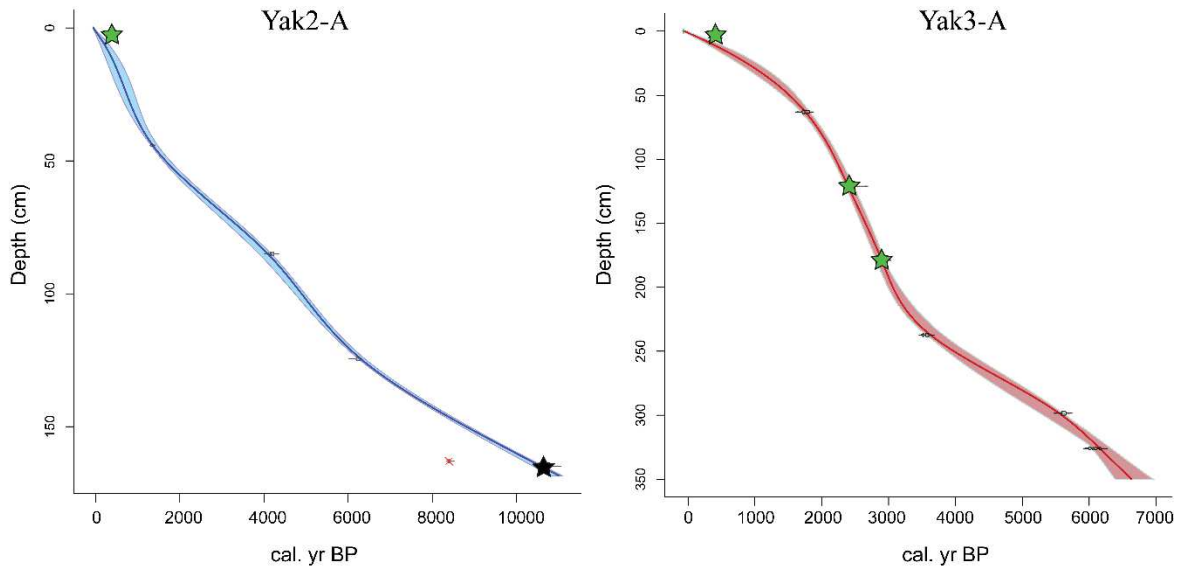


Appendix S3: Google Earth comparison between 1984 (a) and 2016 (b) showing human impact by logging

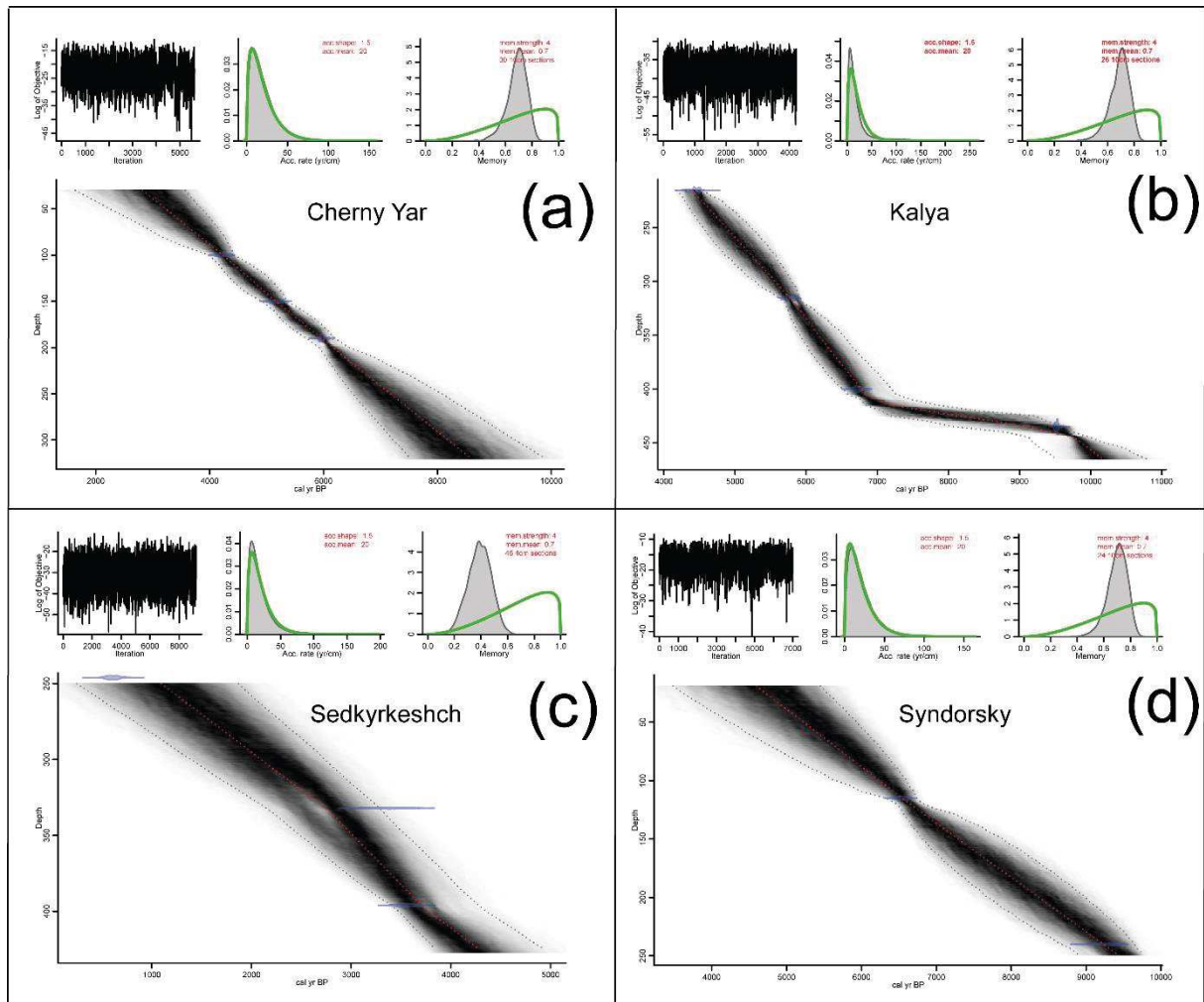
Appendix S4: AMS ^{14}C dating from Yak2-A and Yak3-A (after Barhoumi et al., 2019)

Site	Laboratory. code	Depth (cm)	^{14}C yr BP ($\pm \sigma$)	Materials dated
Yak2-A	ULA-6948	5-5.5	325 ± 15	Plant macroremains
Yak2-A	ULA-6958	45-46	1455 ± 15	Bulk
Yak2-A	ULA-6966	85-85.5	3795 ± 15	Bulk
Yak2-A	ULA-6959	124.5-125	5415 ± 20	Bulk
Yak2-A ^a	ULA-6960	163-163.5	7605 ± 20	Bulk
Yak2-A	BETA-455694	165-165.5	9410 ± 30	Charcoal
Yak3-A	ULA-6967	5-5.5	360 ± 15	Plant macroremains
Yak3-A	ULA-6965	63-63.5	1815 ± 20	Bulk
Yak3-A	ULA-6964	121-121.5	2370 ± 20	Plant macroremains
Yak3-A	ULA-6971	179-179.5	2835 ± 15	Plant macroremains
Yak3-A	ULA-6968	237.5-238.5	3330 ± 15	Bulk
Yak3-A	BETA-455692	298.5-299	4880 ± 30	Bulk
Yak3-A	BETA-455693	326-326.5	5280 ± 30	Bulk

^aAge rejected by the age-depth model



Appendix S5: Age-depth model based on radiocarbon ages (Appendix S4) from Yak2-A and Yak3-A cores. The materials dated to ¹⁴C are bulk (single black lines), plant macroremains (green stars), and macrocharcoal (black star), after Barhoumi et al. (2019). Red star is the age rejected by the age-depth model.



Appendix S6: Winbacon age-depth model based (Blaauw, 2010) on radiocarbon ages from (a) Cherny Yar, (b) Kalya, (c) Sedkyrkeshch and (d) Syndorsky cores (see Tableau IV.1 for references).

Chapitre IV.

INTERACTIONS ENTRE LE CLIMAT, LA VEGETATION ET LES INCENDIES DANS L'OURAL DU NORD (REPUBLIQUE DE KOMI, RUSSIE) PENDANT L'HOLOCENE : UNE APPROCHE MULTI-PROXY

Climate, vegetation and fire interactions in Northern Urals (Komi Republic, Russia) during the Holocene: a multi-proxy approach

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4.1. ABSTRACT

The Holocene climate and its thermal maximum (HTM) have been poorly studied in the northwestern Urals region, particularly in the Republic of Komi, preventing an accurate assessment of the climate-fire-vegetation mechanisms of the Holocene, in the boreal forests of this region. The objective of this study is to reconstruct the Holocene climate (temperatures and precipitation) of the Vychegda River basin of the Republic of Komi, based on the study of pollens, using MAT and WAPLS techniques and comparing it with a temperature reconstruction based on the study of GDGTs (Glycerol Dialkyl Glycerol Tetraethers), which are new biomolecular markers of past temperatures. The results showed that the HTM was between 7000 and 4000 cal. yr BP, which corresponds to a previous study of the region, carried out with another method, and to what is happening in the neighboring Russian and Fennoscandia regions. Furthermore, the calibrations obtained by the GDGTs analysis showed similarities in trends with climate reconstructions from pollen grains study but not temperature values.

Keywords: Boreal Forest ; Peatland ; MAT ; WAPLS ; GDGT, Holocene Thermal Maximum

4.2. INTRODUCTION

Holocene climate trends in Northern Europe, Fennoscandia and Russia have been quantitatively reconstructed from numerous proxies, including chironomids, pollen, stomata or macrofossils records (Seppä et al., 2009, Korhola et al., 2000, 2002; Velle et al., 2005, Nesje et al., 2004). These climate reconstructions generally indicate a marked warming during the Holocene in Northern Europe and Fennoscandia, corresponding to the Holocene Thermal Maximum (HTM) at 8000 cal. yr BP, up to 3500 cal. yr BP (eg Seppä et al., 2009; Salonen et al., 2011).

In contrast, Northern Urals and Komi Republic are poorly documented (Golubeva, 2008). The study of the Vytchegda river basin in the Komi Republic reconstruct a complex climate trend around the Holocene thermal maximum. In this region, the HTM period extended from 6000 to 4800 cal. yr BP (Golubeva, 2008).

Temperature reconstructions in the north of the Vytchegda river basin show different timings for the HTM. Reconstructions of past temperatures in Russian Arctic have shown an HTM similar to Golubeva's study, between 6000 and 4500 cal. yr BP, based on the study of pollen from several lakes (Andreev and Klimanov, 2000). A larger time window has been determined in neighboring areas, with an HTM ranging from 9000 to 5000 cal. yr BP, based on macrofossil studies in the Pechora Delta (Väliranta et al., 2003). An even greater time lag of the HTM was recorded between 10500 and 7500 in Polar Urals based on pollen analysis (Andreev et al., 2005). On the eastern side of the Urals, in western Siberia, an HTM close to that of the Vytchegda river basin was established from pollen analysis, between 6000 and 5000 cal. yr BP (Blyakharchuk and Sulerzhitsky, 1999). Most of these studies are based on pollen data on which quantitative approaches have been used to reconstruct the climate parameters.

In order to better understand the complexity of the climate signal around the HTM, new paleo thermometers can also be used. For example, molecular biomarkers allow to reconstruct the air annual temperature. Temperature biomarker has recently been identified such as the Glycerol Dialkyl Glycerol Tetraethers or “GDGTs”, which are membrane lipid molecules from bacterial origin (Damsté et al., 2000; Weijers et al., 2006). GDGTs are ubiquitous compounds found in oceans, lakes and rivers, peat and soil and the distribution of GDGTs in these environments is partly related to temperature and pH (Weijers et al., 2007a; Peterse et al., 2010). Different calibrations were performed from lakes and peatlands to calculate temperatures based

on GDGTs and branched-GDGTs (br-GDGTs ; Damsté et al., 2000; Weijers et al., 2007a, 2007b; Peterse et al., 2012; Foster et al., 2016; Naafs et al., 2017). However, to our knowledge, these calibrations were not yet used to determine past Holocene temperatures in Russia.

The objectives of this study are (1) to reconstruct quantitatively Holocene temperatures in Republic of Komi (Yaksha core) and in the Vytchegda river basin from pollen data with a multi-method approach, including the Modern Analogs Technique (Guiot, 1990) and the Weighted averaging partial least squares regression (WA-PLS ; ter Braak and Juggins, 1993); (2) to reconstruct Holocene temperatures from the Yaksha sequence with the GDGTs temperature biomarker and test the GDGTs calibration in the Komi Republic ; (3) to provide a robust climate reconstruction for the Holocene period based on pollen and GDGTs in order to discuss the timing of the HTM of this region; (5) to discuss Yaksha's climate dynamics and relate it to Holocene fire and vegetation dynamics (Barhoumi et al., 2019) to highlight the mechanisms that link these three factors .

4.3. MATERIAL AND METHODS

4.3.1. Environmental settings

The Komi Republic is a Russian administrative division of 415 900 km², located on the western side of the Ural Mountains (Figure III.2). The soils of the region are mainly moraine and surface loams (Zaboeva, 1997; Drobyshev et al., 2004), with podzolic soils and the topography is flat except near the Ural Mountains (Naryshkin, 2003). In the North, the mean annual temperature is -6°C, while in the south, it is +1°C and the annual precipitation varies between 450 and 700 mm (Drobyshev et al., 2004a; Golubeva, 2008). The forest cover consists mainly of spruce (*Picea* spp., from 56% regionally in the Komi Republic to 13% locally in Yaksha, within a radius of 10 km. Scots pine (*Pinus sylvestris*, from 25% regionally to 84% locally) and birch (*Betula pendula* and *Betula pubescens*, from 1.4% regionally to 2% locally). Geographical scales therefore opposed the short prevalence of the dark taiga at a regional scale and a clear dominance of a light taiga locally (field observation).

The Northern Urals region in Komi Republic (Russia) is a key climatic zone (Wang et al., 2010; Cheung and Zhou, 2015a). A blocking (Ural Blocking, UB) takes place in this area and can be strong in winter, acting as a barrier to Siberian High during this period, amplifying its effect on

Asian continent and then causing harsher winters (Wang et al., 2010; Cheung and Zhou, 2015b). However, the functioning of this blocking is still poorly understood and documented, and does not allow to anticipate its behavior in the context of the current temperature change (Cheung and Zhou, 2015a).

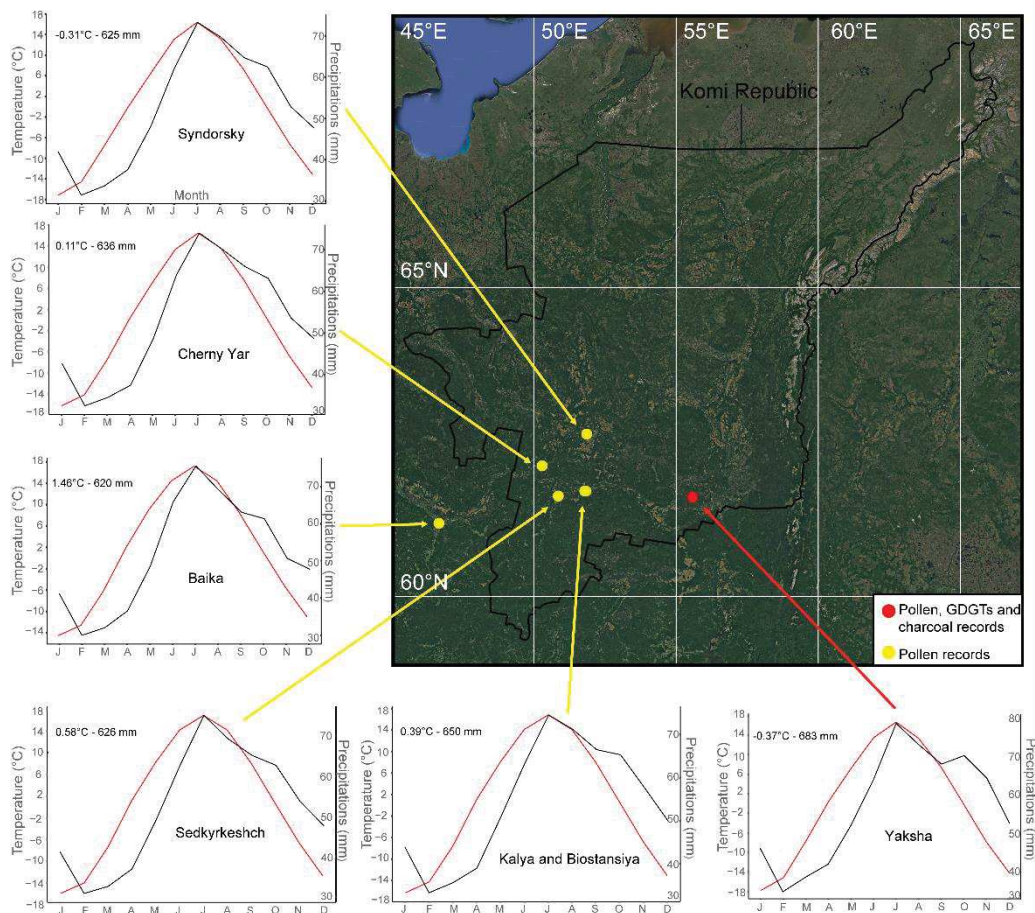


Figure IV.1: Locations of the seven studied sites in the Vychegda river basin of Komi Republic in Russia (black border line). Ombrothermic diagrams of each site (only one for Kalya and Biostansiya sites) were calculated with the New LocClim software program

4.3.2. Study sites

In the Yaksha site, two cores (Yak2-A and Yak3-A) were extracted using an 8-cm diameter Russian peat corer from the center of the Sphagnum peatlands selected (Barhoumi et al., 2019). A composite sequence was built from both cores Yak3-A and Yak2-A (Figure IV.1a). In core Yak3-A, the 0 to 300 cm interval is offering the best temporal resolution and his

very top was preserved (contrary to Yak2-A). Samples were taken every 6 to 10 cm. The bottom sandy part was sterile. Lower part of core Yak2-A offered access to older time interval recorded in organic sediment, although with a lower temporal resolution. Samples were taken every 3 cm. Control samples were taken every 25 cm for the first 100 cm (overlap with core Yak2-A). The chronology was based on five radiocarbon measurements from core Yak2-A, and seven radiocarbon measurements from core Yak3-A and discussed in detail by Barhoumi et al., (2019) (see Appendix SI 1). More details about the Yaksha record are given in Barhoumi et al., (2020). In this study, we used the composite Yaksha record as from Barhoumi et al (2020) for pollen-inferred climate reconstruction and for GDGTs analysis.

Six other pollen sequences located in the same region (Figure IV.1b) are also used to reconstruct the climate to provide the regional climate signal pattern during the Holocene. These cores were reprocessed from south to north: Baika (Borisova, 2002), Sedkyrkesch (Golubeva, 2008), Kalya (Karmanov et al., 2011a), Cherny Yar (Marchenko-Vagapova and Marieva, 2001), Syndorsky (Golubeva, 2008) and Biostansiya (Zaretskaya et al., 2014). Among these six sequences, some of them contain only a part of the Holocene (Tableau IV.1). The Biostansiya pollen record is the only one covering the Late Glacial. If we consider all these sites, we are able to reconstruct quantitatively the climate in the Komi Republic over the last 16,000 years.

Tableau IV.1: Pollen record information for the REVEALS model

Name of the site	Coordinates	Time covered (cal. yr BP)	References
Yaksha	61°43'N, 55°29'E 61°41'N, 55°34'E	-50 – 10,047	This study, (Barhoumi et al., in press)
Baika	61°16'N, 46°44'E	50 - 8775	(Borisova, 2002)
Cherny Yar	62°13N, 50°17'E	2876 - 8532	(Marchenko-Vagapova and Marieva, 2001)

Kalya	61°48'N, 51°47'E	0 - 10150	Karmanov et al., 2011
Sedkyrkeshch	61°43'N, 50°51'E	1197 – 4244	Golubeva, 2008
Syndorsky	62°44'N, 51°51'E	4727 - 9434	Golubeva, 2008
Biostansiya	61°47'N, 51°49'E	12346 - 16836	(Zaretskaya et al., 2014)

4.3.3. Pollen analysis

Peat sequences were divided into 0.5-cm slices. For core Yak3-B, samples were taken every 6 to 10 cm. From core Yak2-A, samples were taken every 25 cm for the first 100 cm (overlap with core Yak2-B) and then every 3 cm. A 3-cm³ subsample of sediment from the center of each slice underwent chemical treatment (HCl, KOH, HF, acetolysis) and 500 µm sieving (Moore et al., 1991). In core Yak2-A, 20 samples were counted and 4 were sterile (no pollen grains preserved). In core Yak3-A, 60 samples were counted and 18 were sterile. The pollen analysis was carried out with a light microscope at a standard magnification of 400x. 39 pollen types were identified using the reference collection at ISEM and photo atlases (Reille, 1992, 1998; Beug, 2004). Two *Pinus* species (i.e. *sibirica* and *sylvestris*) were identified while *Betula* spp. (*pendula* and *pubescens*) and *Picea* (*abies* and *obovata*) subspecies were not distinguished. A minimum of 300 pollen grains was counted per sample, and the average sum was 315 pollen grains. Pollen percentages based on the total pollen sum were calculated, excluding Cyperaceae (see Appendix SI 1).

More details about the Yaksha pollen record are given in Barhoumi et al (accepted); only the main changes are summarized here. Pollen assemblages from Yaksha (Figure IV.3) were divided into 4 pollen zones labeled Z'1, Z'2A, Z'2B and Z'3 (Appendix SI 1). The pollen diagram indicates a forested landscape during the last 10,000 years. From 10 000 cal. yr BP to 6050 cal. yr BP, the vegetation was dominated by *Pinus sylvestris* and *Betula*. These two taxa opposed: when *Pinus sylvestris* decreases, *Betula* increases. *Picea* was also recorded and showed close trends as *Pinus sylvestris*, while *Abies* and *Pinus sibirica* were absent during this

period. Therefore, this period ranked today's description of a light taiga system. *Sphagnum* spp. related to the peatland itself where it developed on peat surface and wet soils. The percentage of wetland taxa Cyperaceae, temporarily increases between 9000 and 7800 cal. yrs BP. The zone Z'-2 extends from 6050 BP to 100 cal. yr BP and was characterized by an increase of *Picea* and the appearance of *Pinus sibirica*. It was divided into two subparts, Z'-2A from 6050 to 3200 cal. yr BP and Z'-2B from 3200 to 100 cal. yr BP. *Pinus sylvestris* and *Betula* showed different patterns and their relationship was more complex. *Pinus sibirica* appeared in Z'-2A and *Abies* in Z'-2B, signaling the establishment of a dark taiga forest. From 3200 to 100 cal. yr BP (Z'-2-B), the dark taiga decreased slowly and the light taiga reappeared, with the increase of *Pinus sylvestris*. More recently, there was a strong increase in *Betula*, which reached percentages above 65% (Z'3, from 100 cal. yr BP to 0 cal. yr BP).

4.3.4. Pollen-inferred climate reconstructions: a multi-method approach

The reconstruction of mean annual temperatures (TANN), annual sum of precipitation (PANN) (Figure IV.2) and temperatures of the warmest month (MTWA) and coldest months (MTCO) and sums of summer precipitations (PSUM) (Appendix SI 5), were performed with two different methods, in order to increase the reliability of our reconstruction: the Modern Analogue Technique (MAT ; Guiot, 1990) and the Weighted Averaging Partial Least Squares Regression (WA-PLS ; ter Braak and Juggins, 1993).

The MAT compares modern pollen assemblages, whose climatic parameters are known, with fossil pollen assemblages with square string distance, which determines the degree of efficiency of the similarity between samples. The smaller the distance from the chord, the greater the similarity between the samples. For each fossil sample, the climate parameters are calculated as a weighted average of the current climate index of the nearest similar samples. A similar threshold is established using a Monte Carlo method.

WAPLS is a regression method that also assumes that the relationships between pollen percentages and climate are unimodal. For each taxon there is an optimal climate variable value. The modern pollen data set used can be considered as a large multidimensional matrix. Since there is collinearity between pollen taxa and some taxa are linked to climatic parameters of interest, it is possible to reduce the data set to a reduced number of components based on the linear predictors of the parameter of interest and on the residual structure of the data when these predictors are removed (Peyron et al., 2013).

Both methods are based on a modern pollen dataset. The dataset used here to determine the past climate at Yaksha is a sub-dataset from an Eurasian database, with more than 3000 sites (Peyron et al., 2013). The sub-dataset including 2115 sites was determined by selecting sites characterized by a biome comparable to the Yaksha biomes. The biomes selected were Anthropological environments, Cold Deciduous Forest, Cold Mixed Forest, Cold Coniferous Forest, Cold Mixed Forest, Cold Steppes Forest, Pioneer Environments, Taiga forest and Tundra.

4.3.5. GDGT measurements

A total of 26 samples from Yak3-A and 12 samples from Yak2-A were proceeded for GDGT analyses at ENS Lyon (LGLTPE, France). Samples were freeze-dried and grounded. In aliquots of less than a gram, a C₄₆ standard solution, at 10 ng.μL⁻¹ was added (Huguet et al., 2006). Then, lipids were microwaved (MARS, CEM), with dichloromethane (DCM):MeOH (3:1). Total lipid extracts were separated into polar and apolar fraction on an Al₂O₃ alumine column (1 g) with hexane:DCM (1:1) and DCM/MeOH (1:1). The fractions were then analyzed by a High Performance Liquid Chromatography Mass Spectrometer (HPLC-MS, Agilent 1200) (Hopmans et al., 2016; Davtian et al., 2018).

Reproducibility of the measurements was calculated by replicated analyses of two samples of the sediment core.

4.3.5. GDGT indices and temperature reconstructions

Br-GDGT (Appendix SI 2) abundances were combined into several indices (Tableau IV.2) such as the Branched and Isoprenoid Tetraether Index (BIT - Hopmans et al. (2004), the Cyclization ration of Branched Tetraethers (CBT - Weijers et al., 2007a) and the Methylation of Branched Tetraether (MBT' - Peterse et al., 2012 and MBT'_{5Me} - De Jonge et al., 2014b).

Temperature reconstructions were based upon several indices: the Methyl Index of Branched Tetraether (MBT - (Weijers et al., 2007a). It has been modified by Peterse et al. (2012) with MBT' and by Naafs et al. (2017) with MBT'_{5Me} excluding br-GDGTs 6-methyl. The calibration of the Mean Air Temperature (originally MAT, hereafter called MAT_{Peterse}) was calculated by Peterse et al. (2012) from their ownsoil GDGTs dataset. Given the range of temperature

variations in the site considered, we tested the calibration equation developed for high latitudes: a calibration of the mean summer air temperature (MSAT), calibrated for high latitudes, from GDGTs from Antarctic lakes was determined by Foster et al (2016). A calibration of the mean annual air temperature, calibrated for the GDGTs located in peatlands (MAAT_{peat}), was determined by Naafs et al (2017).

Tableau IV.2: Formulas of the indices and temperature calibrations based on the br-GDGT fractional abundances

Indices/Temperature calibrations	Formula	References
BIT	$= \frac{Ia + IIa + IIIa + IIIa' + IIIa'' + IIIa''' + IIIa7Me + IIIa7Me}{Ia + IIa + IIIa + IIIa' + IIIa'' + IIIa''' + IIIa7Me + IIIa7Me + C7}$	(Hopmans et al., 2004)
CBT	$= -\log\left(\frac{Ib + IIb + IIIb6Me}{Ia + IIa + IIIa6Me}\right)$	(Weijers et al., 2007a)
MBT'	$= \frac{Ia+Ib+Ic}{Ia+Ib+Ic+IIIa'+IIIa''+IIIa''' + IIIa7Me + IIIb' + IIIb'' + IIIc' + IIIc'' + IIIa' + IIIa'' + IIIb' + IIIb'' + IIIc'}$	(Peterse et al., 2012)
MBT' _{5Me}	$= \frac{Ia + Ib + Ic}{Ia + Ib + Ic + IIa + IIb + IIc + IIIa}$	(De Jonge et al., 2014)
MAT _{Peterse}	$= 0.81 - 5.67 \times CBT + 31.0 \times MBT'$	(Peterse et al., 2012)
MSAT	$= 18.7 + (80.3 \times Ib) - (25.3 \times IIa) - (19.4 \times IIIa) + (369.9 \times IIIb)$	(Foster et al., 2016)
MAAT _{peat}	$= 52.18 \times MBT'_{5Me} - 23.05$	(Naafs et al., 2017)

4.4. RESULTS

4.4.1. Pollen-inferred climate patterns

The Biostansiya pollen record is the only one which covers the Late Glacial. It shows dryer than today conditions from 16500 to 12500 cal yrs BP associated to very cold annual temperatures (between -13 and -4°C), which were lower than today and lower to the temperatures values inferred from the other sites during the Holocene (Figure IV.2). Colder than today conditions are clearly reconstructed during the Late Glacial period, however, it is of note some differences in climate trends depending on the method. With the MAT, results show cold conditions while at 16000 cal BP, a strong warming at 15000 cal BP and a cooling around 12500 cal yrs BP. With the Weighted Averaging Partial Least Squares Regression, results show temperature and precipitation increase around 16000 cal. yr BP and a cooling around 12500 cal yrs BP (Figure IV.2).

During the Holocene, the mean annual temperature (TANN) reconstructed with the Modern Analogue Technique and the Weighted Averaging Partial Least Squares Regression from the different cores (Yaksha, Baika, Kalya, Cherny Yar, Sedkyrkeshch and Syndorsky) is broadly similar in terms of trends and amplitude (Figure IV.2). Yaksha, Baika and Kalya are considered here as “key” sites because they cover almost the entire Holocene to modern times; moreover, for these sites, the temperatures values reconstructed for the most recent samples are very close to the measured modern values (-0.37°C at Yaksha, 1.46°C at Baika and 0.39°C at Kalya). For the Yaksha, Baika, Cherny Yar, Sedkyrkeshch and Syndorsky sites, the temperature trends reconstructed with the MAT and the WAPLS methods are similar. However, for Kalya the temperature trends reconstructed with both methods are similar only from 5500 to 0 cal BP. (Figure IV.2). With regard to the reconstruction of TANN, the results from the Yaksha, Baika and Kalya sites show an HTM extended between 7000 cal. yr BP and 4000 cal. yr BP, with both methods and warmer temperature values from 1°C (WAPLS) to 3°C (MAT). From 4000 to 3000 cal. yr BP, our results show a general decrease in temperatures, with values lower than today. Then, from 3000 to 0 cal. yr BP, the temperatures rise gradually and reach the current values.

Concerning PANN reconstructions, there is a gradual increase throughout the Holocene with oscillations around the modern value (about 630 mm/year).

For the records which contain only part of the Holocene, results seems to follow the same climate trend. At Cherny Yar, the temperatures decrease from 8700 to 6500 cal. yr BP, then rise and remain high until 3000 cal. yr BP. The HTM is reached at 5000 cal. yr BP. PANN reconstructions continually increase from 600 mm at 8700 cal. yr BP to about 900 mm at 3000 cal. yr BP. At Serdyrkeshch, we reconstruct a gradually increase in temperature from 4000 to

1000 cal. yr BP and precipitations fluctuate around modern values. At Syndorsky, temperatures fluctuate around 2°C and the maximum value is reached at 8000 cal. yr BP while precipitations fluctuate around modern values.

Reconstructions of temperature of warmest months, coldest months and sum of summer precipitation were also performed to discuss more in depth the seasonality of the climate signal reconstructed and to compare with the GDGTs climate signal (Appendix SI 5). Summer and winter temperature reconstructions show similar trends to those of TANN with an HTM ranging from 7000 to 4000 cal. yr BP. Summer precipitation shows higher values than the modern value from about 7000 cal. yr BP.

4.4.2. GDGT abundances and indices

Within the Yaksha site, the majority of br-GDGTs are tetramethylated forms Ia (48%) and pentamethylated forms IIa (39%) (Figure IV.3). The hexamethylated form IIIa represent 6% of the total brGDGTs. The remaining br-GDGTs are present at values below 2%. The average BIT index is 0.998 ± 0.005 .

The CBT, MBT' and MBT'_{5Me} indices vary in the same way and present the same dynamics across the Holocene (Appendix SI 3). The variations of these indices are small over the first half of the Holocene, from 10000 to 5500 cal. yr BP. Then from 5000 to 2000 cal. yr BP, the variations are more pronounced and from 1000 to 0 cal. yr BP, the variations become less strong again. The CBT range from 1.5 to 1.8 from 10000 to about 5500 cal. yr BP, with an increasing phase between 9700 and 9000 cal. yr BP and between 7700 and 7000 cal. yr BP (CBT values at 1.7 and 1.8, respectively). Then from 5500 to 1000 cal. yr BP, the variation range increases and the CBT values range from 1.2 to 2.1, with an optimal phase between 4000 and 2000 cal. yr BP. From 1000 to -32 cal. yr BP, the CBT decreases and the values range between 1.2 and 1.6. MBT' and MBT'_{5Me} values are very close. From 10000 to 9400 cal. yr BP they increase from 0.47 to 0.55. Then they decrease to 0.38 at 8900 cal. yr BP. Then, up to 5500 cal. yr BP, the values vary slightly around 0.5. They then decrease to 0.40 to 5000 cal. yr BP and then rise to 0.62 to 4000 cal. yr BP. The values remain optimal up to 3000 cal. yr BP then decrease and vary slightly around 0.5 until the end of the signal.

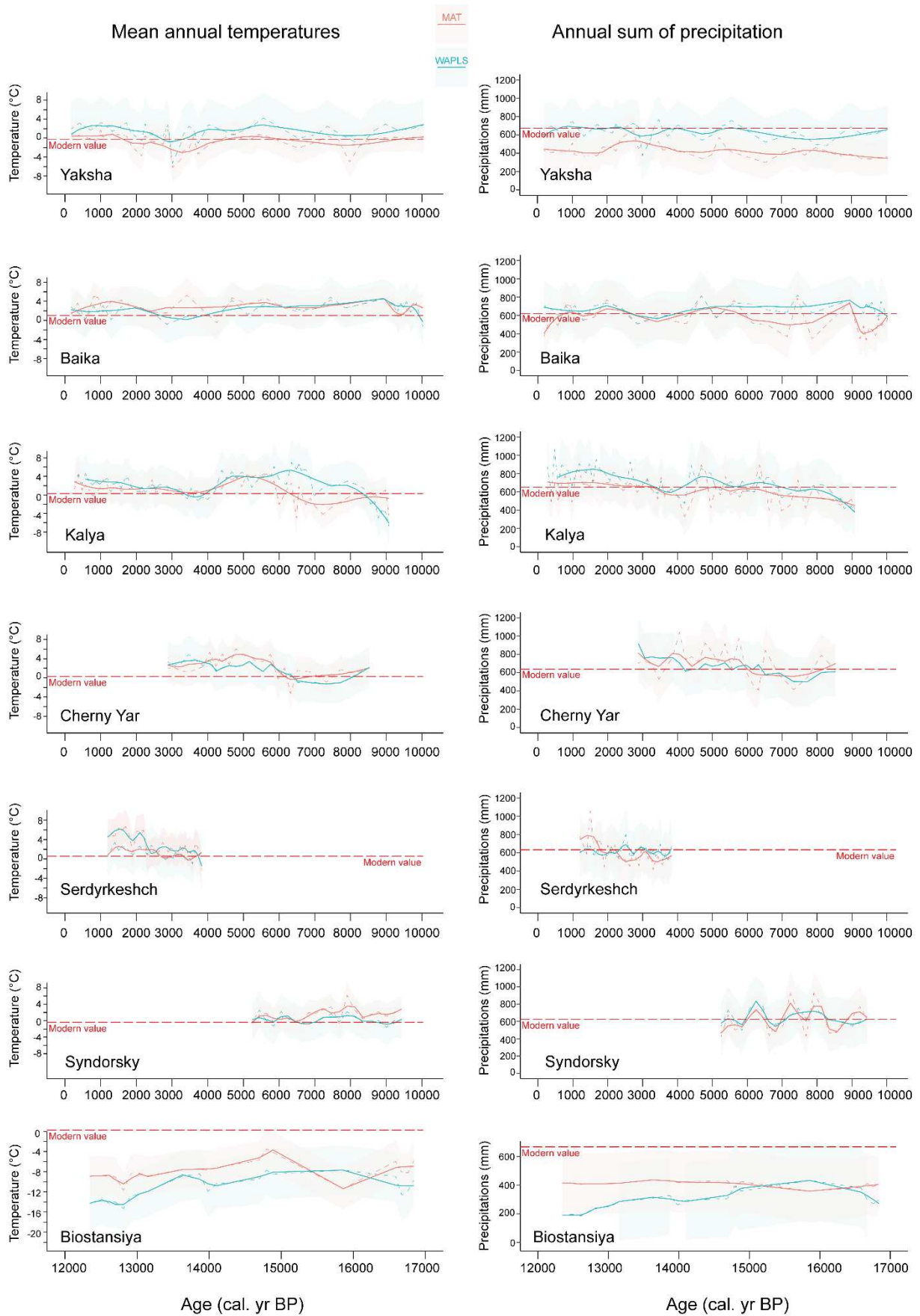


Figure IV.2: Komi Republic Pollen-based climatic parameters, dashed lines (Mean annual temperature and annual sum of precipitations) calculated with the modern analogue technique (MAT) and the weighted-average partial least-squares regression (WAPLS) and smoothed, solid lines, with Loess (span = 0.3). Shaded areas are confidence interval. Red dashed lines are modern values, for each site (NewLocClim).

4.4.3. GDGT temperature reconstruction

Three temperature calibrations have been tested for the Yaksha core (Figure IV.4) (Peterse et al., 2012; Foster et al., 2016; Naafs et al., 2017). The reconstructed temperatures range between 6 to 11°C, 4 to 10°C and -2 to 10°C, respectively. The three reconstructions show similar pattern, with a decrease (of 1°C) at the beginning of the Holocene, from 10000 to 9000 cal. yr BP. However, the MAAT_{peat} calibration shows more marked trends than the others. Then temperatures increase from 9000 to 7000 cal. yr BP before decreasing again to 5000 cal. yr BP. From 5000 cal. yr BP, temperatures rise and reached an optimum, which extends to 2500 cal. yr BP. The optimal values in MAT_{Peterse} are 11°C at 4000 cal. yr BP, for MSAT, 11°C at 3500 cal. yr BP and for MAAT_{peat}, 11°C at 3500 cal. yr BP. Temperatures decrease to 1800 cal. yr BP, then increase again to modern time. The temperature values from the calibrations are much higher than the current value, it is therefore more interesting to discuss trends, rather than values.

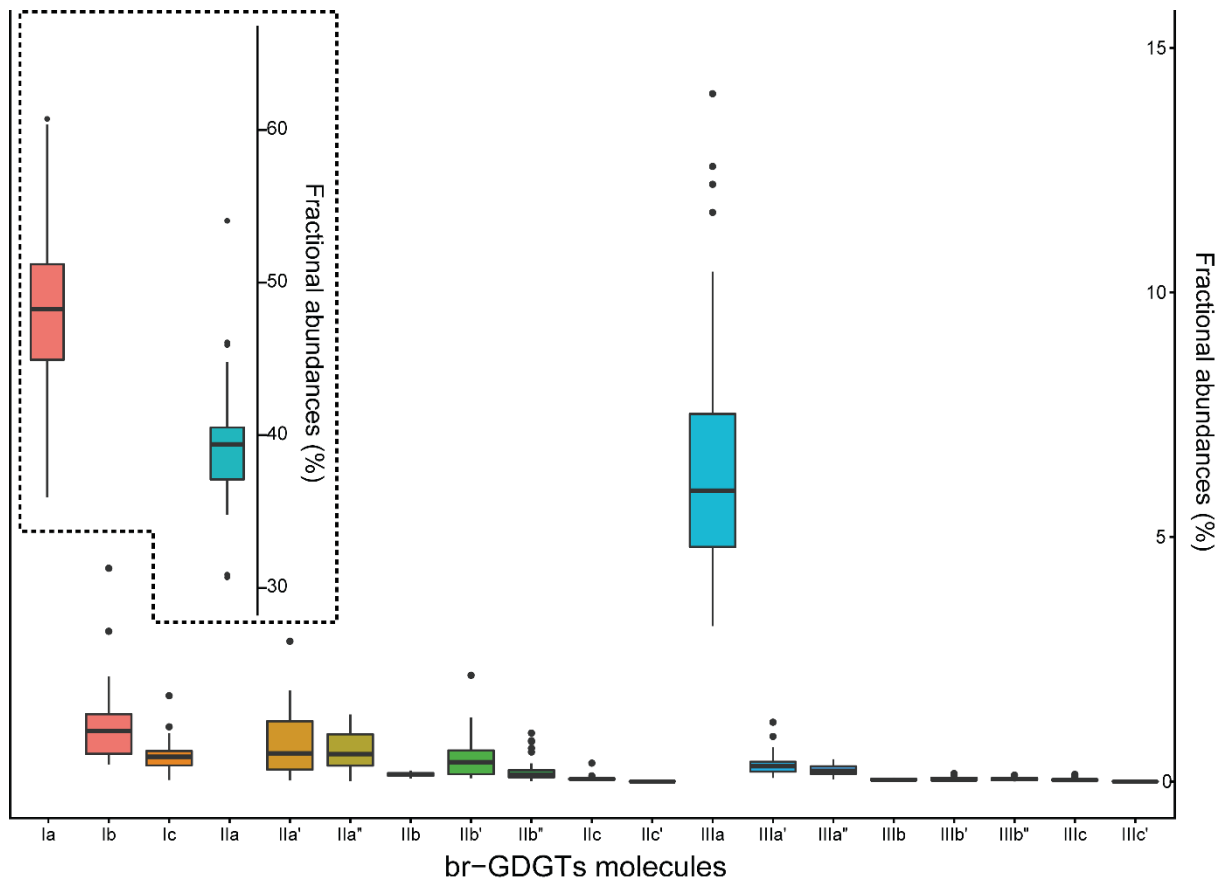


Figure IV.3: Fractional abundance for each Yaksha br-GDGTs represented against two % scales.

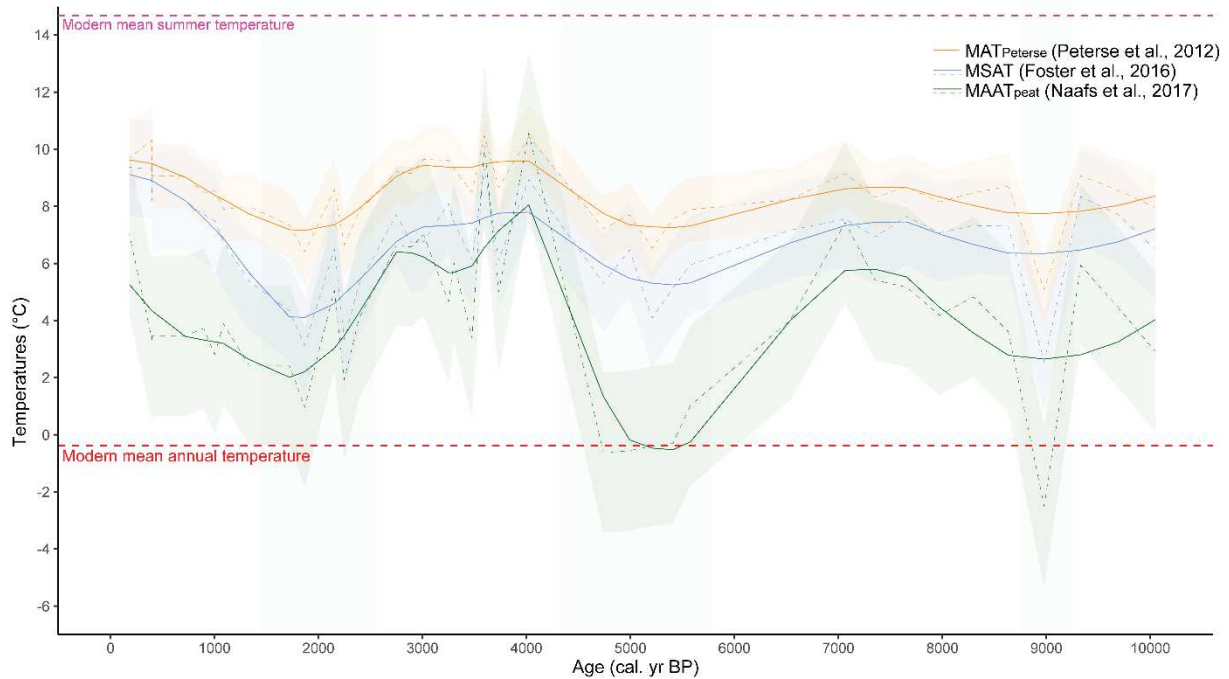


Figure IV.4: Yaksha GDGT temperature reconstruction. Blue: $MAT_{Peterse}$ after Peterse et al. (2012), orange: the MSAT after Foster et al., (2016), and green: $MAAT_{peat}$, after Naafs et al. (2017). The reconstructed temperatures are smoothed with Loess (span = 0.3), represented with solid lines. The horizontal shaded areas represent the standard deviations. The red dashed lines represent the modern mean annual temperature value of Yaksha inferred from NewLoclim (-0.37°C). The vertical shaded areas represent the cold stages of the Holocene.

4.5. DISCUSSION

4.5.1. Assessment of GDGT temperature calibrations

None of the three calibrations shows values for the 0 cal. yr BP close to the modern mean annual temperature at Yaksha (-0.37°C). Temperature values are higher than the modern ones: the $MAT_{Peterse}$ reconstructed values are 9°C , MSAT 9.4°C and $MAAT_{peat}$ 5.9°C . Br-GDGTs individual abundances from Yaksha's br-GDGTs dataset are homogeneously integrated into Naafs et al. (2017)'s (Appendix SI 4). This calibration is therefore appropriate for the reconstruction of the temperature based on the GDGTs of Yaksha, which is a forest peatland. However, although $MAAT_{peat}$ values are the closest to modern values, the window of

variability is much larger than with the other two calibrations and should therefore be carefully interpreted.

4.5.2. Assessment of MAT/WAPLS pollen-based temperatures

Remarkably similar climate trends are reconstructed for the Holocene with the two methods, MAT and WAPLS (Figure IV.2). However, the trends diverge in terms of variability: the MAT method generally indicates less variability than the WAPLS method, as it has been already observed in other studies (Birks and Seppä, 2004). During the Late Glacial period, colder than today conditions are clearly inferred from both methods however, only the temperature reconstructed with the MAT follow a “classical” Lateglacial pattern: cold conditions during the oldest Dryas at 16000 cal BP, strong warming at 14700 cal BP corresponding to the Bolling warming and a cooling probably corresponding to the Younger Dryas around 12500 cal yrs BP (Figure IV.2). These results are particularly promising because the MAT method is usually more sensitive than the WAPLS (Brewer et al., 2008; Sinopoli et al., 2019) but may be less efficient than transfer functions (as WAPLS) when the vegetation is only dominated by two or three taxa, as is the case in our study (Salonen et al., 2012). In general, WAPLS is favored to quantify Holocene temperatures in the boreal regions of Scandinavia (Seppä et al., 2009a; Salonen et al., 2011, 2012). The WAPLS method performs less when the data set is large (continental for example), but in this study it was reduced to those regions that most closely approximated the climatic and vegetation conditions of the study sites, which is also recommended to increase the sensitivity of the MAT method (Birks and Seppä, 2004). Results show that here in the Komi republic, both methods are reliable and provide similar trends for the Holocene and that the MAT provides more accurate results for the Lateglacial.

4.5.3. Climate reconstruction: Yaksha GDGTs-based temperatures vs MAT/WAPLS pollen-based temperatures

The comparison between the reconstruction of pollen-based temperatures (MAT and WAPLS) with those of the GDGTs-based (Figure IV.5) shows (1) in general, similar trends from 5000 cal. yr BP, (2) values and amplitudes of variations that are very different, especially at the HTM period and which are more marked with the GDGTs-based reconstructions.

Pollen and GDGTs-inferred temperature reconstructions indicate an upward trend in temperature between 8500 and 7000 cal. yr BP (3°C with WAPLS, 1°C with MAT and 7°C with $\text{MAAT}_{\text{peat}}$). From there, the temperature reconstructed from pollen and GDGTs shows important discrepancies in their amplitude: $\text{MAAT}_{\text{peat}}$ signal decreases sharply to 4500 cal. yr BP (-0.5°C), while pollen-inferred temperature reconstruction shows a smaller decrease.

The HTM period, according to pollen-based reconstructions, occurred between 7000 and 4000 cal. yr BP. With the GDGTs-based reconstructions based on the $\text{MAAT}_{\text{peat}}$ calibration, the duration of the HTM period seems longer, from 8500 to 3000 cal. yr BP and a strong cooling is depicted at 5500 cal. yr BP. In detail, two warming periods are observed during the Holocene, the first between 8500 and 6500 cal. yr BP. The second warm period is recorded between 4500 and 3000, with an optimum higher than the previous one, around 11°C . Considering the large range of variability from $\text{MAAT}_{\text{peat}}$, previously discussed, and compared to $\text{MAT}_{\text{Petersen}}$ and summer signal (MSAT calibrations which also indicate a decrease of temperatures between 7000 and 5500 cal. yr BP, but with higher values than the lowest values of temperatures at the end of the Holocene), one could consider that the HTM based on GDGTs ranges from 8000 to 3000 cal. yr BP, similar to the study by Salonen et al. (2011), and shows a wider extension window than the one based on pollen. The observed decrease in temperatures between 7000 and 5500 cal. yr BP, indicated by the three GDGT calibrations, could result from a sensitive bias from GDGTs to cold temperatures, as suggested by Naafs et al. (2017), who argue that seasonal biases may exist in peatlands at high latitudes, and by Martin (2018) who suggests this hypothesis in her analysis from Lake Saint-Front (France), regarding non-synchronous HTM between GDGTs and pollen signals.

From 3500 cal. yr BP onwards, both the pollen-inferred climate temperature and the GDGTs- $\text{MAAT}_{\text{peat}}$, show a period of high variability of temperatures, up to about 2000 cal. yr BP. The different temperature increases/decreases seems also slightly offset between the pollen signals and the GDGTs signal. The end of the Holocene (from 1000 cal. yr BP to modern time) corresponds to more stable temperatures around 2°C with WAPLS and 0.5°C with MAT. With $\text{MAAT}_{\text{peat}}$, the end of the Holocene is characterized by a gradual increase in temperatures, from 1°C to 2000 cal. yr BP, to 7°C to -32 cal. yr BP. This late Holocene warming recorded by the GDGTs is not close to modern temperatures values in Yaksha and is further away than the pollen-based signal. However, the dynamics of temperature increase over the past 2000 years recorded by GDGTs, has also been observed in the Kola Peninsula in Northern European Russia (Hiller et al., 2001 - wood macrofossils analysis), and may indicate that GDGTs are more

sensitive than pollen in detecting the recent increase of the temperature, since the pollen signal did not show any warming.

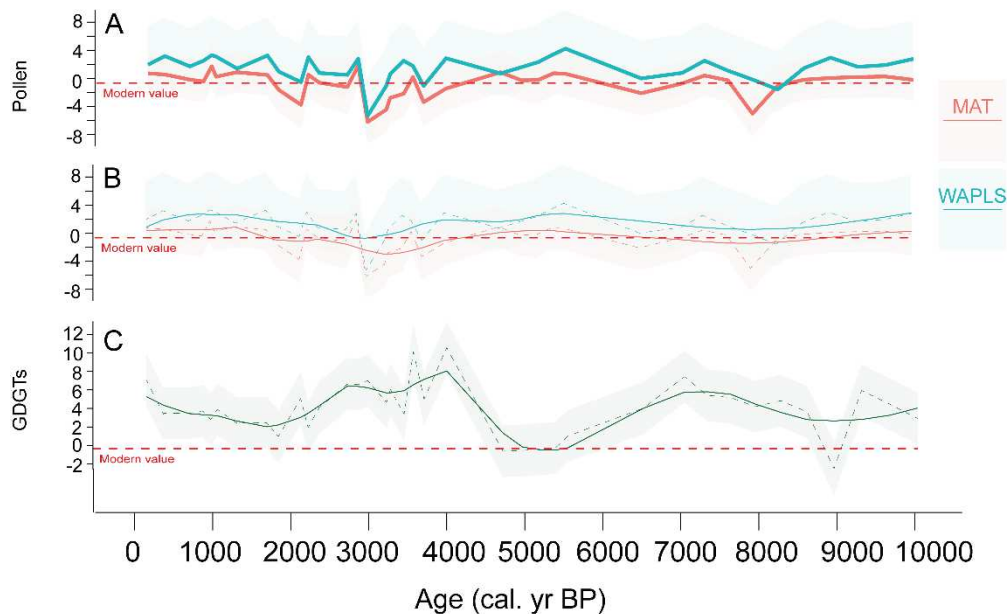


Figure IV.5: Yaksha temperatures reconstructions. (A) Pollen-inferred temperature of the mean annual temperature with MAT and WAPLS (bold lines). (B) Pollen-inferred temperature of the mean annual temperature with MAT and WAPLS (dashed lines) and the smoothed signal (solid lines). (C) Yaksha GDGT temperature reconstruction $MAAT_{peat}$.

4.5.4. Comparison of climate reconstructions with neighbouring regions

In the Komi republic, the mid-Holocene is characterized by the occurrence of HTM between 7000 and 4000 cal. yr BP in Yaksha, Baika, Kalya, and Cherny Yar. Most sites show a duration for the HTM of 2500-year, with some differences in the timing of about 500 years from one site to another, but for all sites, a common period ranging from 7000 to 4000 cal. yr BP is recorded. This HTM time window is quite consistent but broader with those found by Golubeva (2008), with the same pollen dataset (except Yaksha) but with another method (Figure IV.5), the Klimanov's method (Klimanov, 1976) which is based on the assumption that pollen spectra and climate conditions are linked by a linear correlation equation (Klimanov, 1976; Andreev and Klimanov, 2000). This extension of HTM reconstructed with MAT/WAPLS techniques is consistent with the Russian Arctic region reconstructions (Tarasov et al., 1999;

Andreev and Klimanov, 2000), in the north of the Komi Republic; but also to the east of the study area, in Western Siberia and in central Yakutia (Blyakharchuk and Sulerzhitsky, 1999; Ulrich et al., 2017). The Russian Arctic HTM was explained because the Arctic Ocean coast was about 100 to 300 km further north at this time than it is today, which contributed to a warmer and more continental climate (Andreev and Klimanov, 2000). However, in Siberia, from 10,000 cal. yr BP until 4000 cal. yr BP, climate was the moistest of the Holocene (Blyakharchuk and Sulerzhitsky, 1999; Tarasov et al., 1999), which was not the case on the western side of the Urals, in Komi Republic, where rainfall fluctuated around a stable value compared to the end of the Holocene (Yaksha, Baika and Syndorsky sites), or was even lower than at the end of the Holocene (Kalya and Serdyrkeshch sites). HTM in the Komi Republic extended less than in northern Europe and Fennoscandia, where it began as early as 8000 cal. yr BP (Seppä et al., 2009a; Salonen et al., 2011). Another delayed HTM was observed by Kultti et al. (2003), yet closer to Komi Republic, between 9000 to 5200 cal. yr BP. Some of the sites in this study were located at high altitude in the Urals. The altitude may have had an impact on the different climatic influences affecting the area from Arctic Russia to the Vychegda river basin in Komi Republic. Many studies highlight the role of increased insolation in global warming during the HTM (Kultti et al., 2003; Mayewski et al., 2004; Wohlfarth et al., 2007; Bartlein et al., 2011). Climatic influences are also hypotheses that explain this warming phase: a strong westerly circulation, with a strong AO/NAO positive phase in winter (which generated warm and moist climate in northern Europe) and a weaker AO/NAO positive phase in summer (warm and dry climate) (Mauri et al., 2015). Studies have also discussed the observed lags in HTM from Fennoscandia to the Ural region (Salonen et al., 2011). The hypotheses put forward are (1) there is a timing gradient of the HTM. (2) some reconstructions may be wrong due to biases in the used temperature inference method. (3) The different proxies for calculating temperatures may have non-synchronous responses to warming. (4) The complex history of treeline in Russia may add uncertainties regarding pollen-based reconstructions.

After the HTM, a fluctuating and colder phase is marked in Komi Republic between 4000 and 3000 cal. yr BP. In Arctic Russia (Andreev and Klimanov, 2000), this phase was related to the strong influence of the AO. Temperatures were correlated to precipitation. In Northern Europe Russia, the cooling was marked between 3500 and 2000 cal. yr BP and explained by the decrease in insolation (Salonen et al., 2011). According to Seppä et al. (2009), the Medieval Warm Period is not a distinct peak in Northern Europe but the Little Ice Age was also marked from 800 cal. yr BP. At the end of the 19th century, a global warming has been

recorded by tree-rings in northern Urals (Moiseev et al., 2010) but in Komi Republic, the results did not show any warming during this period (only the site Yaksha dates back to this period), probably due to the human impact on the management of this region during this period (Drobyshev et al., 2004b; Karmanov et al., 2011b; Klein Goldewijk et al., 2011).

The Late-Holocene (from 3000 to 0 cal. yr BP) is characterized by an increase in temperatures (following the decrease that marks the end of the HTM) towards modern values at all sites. This consistency between modern values and reconstructed values for recent times increases confidence in temperature reconstruction with these methods.

4.5.5. Lateglacial climate

The Biostansiya record is the only one in the Komi republic to cover the Late-Glacial period, before the Holocene. For the Late-Glacial interstadial, much lower temperatures than those reconstructed during the Holocene are evidenced (from -14°C to -4°C). The first remarkable event depicted here is a strong warming between 15000 and 14500 cal. yr BP. This event can be related to the warming of the Bölling (Peteeet, 2000; Yu and Eicher, 2001). The second remarkable event is a cooling from 13000 cal. yr BP until the end of the record. This event may be related to the Younger Dryas cold event depicted in numerous records of Europe and other regions (Dansgaard et al., 1989; Snyder et al., 2000; Carlson, 2010). The main explanation for this event is a slowdown in the AMOC (Carlson, 2010).

In the Vytchegda river basin, the Lateglacial period was characterized by low annual temperatures (between -16 and -8°C) and extremely low precipitation (around 300 mm), compared to the Holocene (Golubeva, 2008). The climate was similar in the pre-Polar Urals region (Golubeva and Kryazheva, in press), from a study based both on pollen and microterea fauna. This study shows also evidences of the Bolling-Allerod warming, which is therefore observed on both slopes of the Urals (between 15000 and 14500 cal. yr BP). To the north of the study area, but over the western Ural region, Andreev and Klimanov, (2000) showed that Younger Dryas took place between 12800 and 11400 cal. yr BP, which is consistent with current results of the Republic of Komi. This cooling phase was recorded between 12250 and 11500 cal. yr BP in northern Norway (Birks et al., 2014; based on pollen and chironomids analysis), with a July temperature close to the summer temperatures of the Republic of Komi for this period.

4.5.6. Occurrence of the 8.2 ka ?

In terms of patterns, the beginning of the Holocene is characterized by a slight decrease in temperatures. However, the significant drop in temperatures between 8000 and 8200 cal. yr BP with pollen-based inferred temperatures (-5°C with MAT, -2°C with WAPLS, Figure IV.6) seems to occur earlier with the GDGTs reconstruction (-2°C at 9000 cal. yr BP). Pollen and brGDGTs probably do not record the same event given that the sudden decrease in $\text{MAAT}_{\text{peat}}$ is marked with only one GDGTs sample, and should therefore be interpreted with caution; The 8200 cal. yr BP cooling event, may be evidenced at Yaksha, was studied and discussed in detail for Northern Europe (Seppä et al., 2007, 2009a). The hypotheses put forward by Seppä et al (2007) are (1) the cold air resulting from the cold water flow that disrupted the AMOC, which was probably the major forcing of this event was weakly transported to the North because of a weak NAO mode resulting to an expansion of sea ice in the North Atlantic and therefore a decrease in heat advection. (2) Cooling took place mainly in Winter, and therefore had little impact on the phenology of cold forest trees. These assumptions can be used to explain that the 8200 cal. yr BP event was not recorded by all the study sites, which are located north of 61°N . In Yaksha, a more marked decrease between 8200 and 8000 cal. yr BP may be related to event 8200 cal. yr BP (Alley et al., 1997). However, this cooling is only observable for temperature reconstruction at Yaksha and does not appear to have been expressed through the Baika, Kalya and Cherny Yar reconstructions A slight cooling occurs at Syndorsky at the same time, but temperatures remain in the global range.. So here too, the occurrence of the 8.2 ka event in Komi republic must be interpreted with caution. There are several reasons to explain why all sites don't show a cooling to 8200 cal. yr BP. The Kalya site presents four radiocarbon dates for the entire Holocene period, which is relatively low and therefore increases the uncertainty of the age model. In Baika, the resolution is about 200 to 300 years between each sample, which generates enough time for an event of this scale to be hidden. Finally, an hypothesis put forward by Seppä et al. (2007) suggests that cooling to 8200 cal. yr BP may have occurred in winter and early spring. Pollen production from taxa in boreal zones (mainly *Pinus* spp., *Picea* spp. and *Betula* spp.) may not have been significantly affected, since they are highly resistant to cold climates.

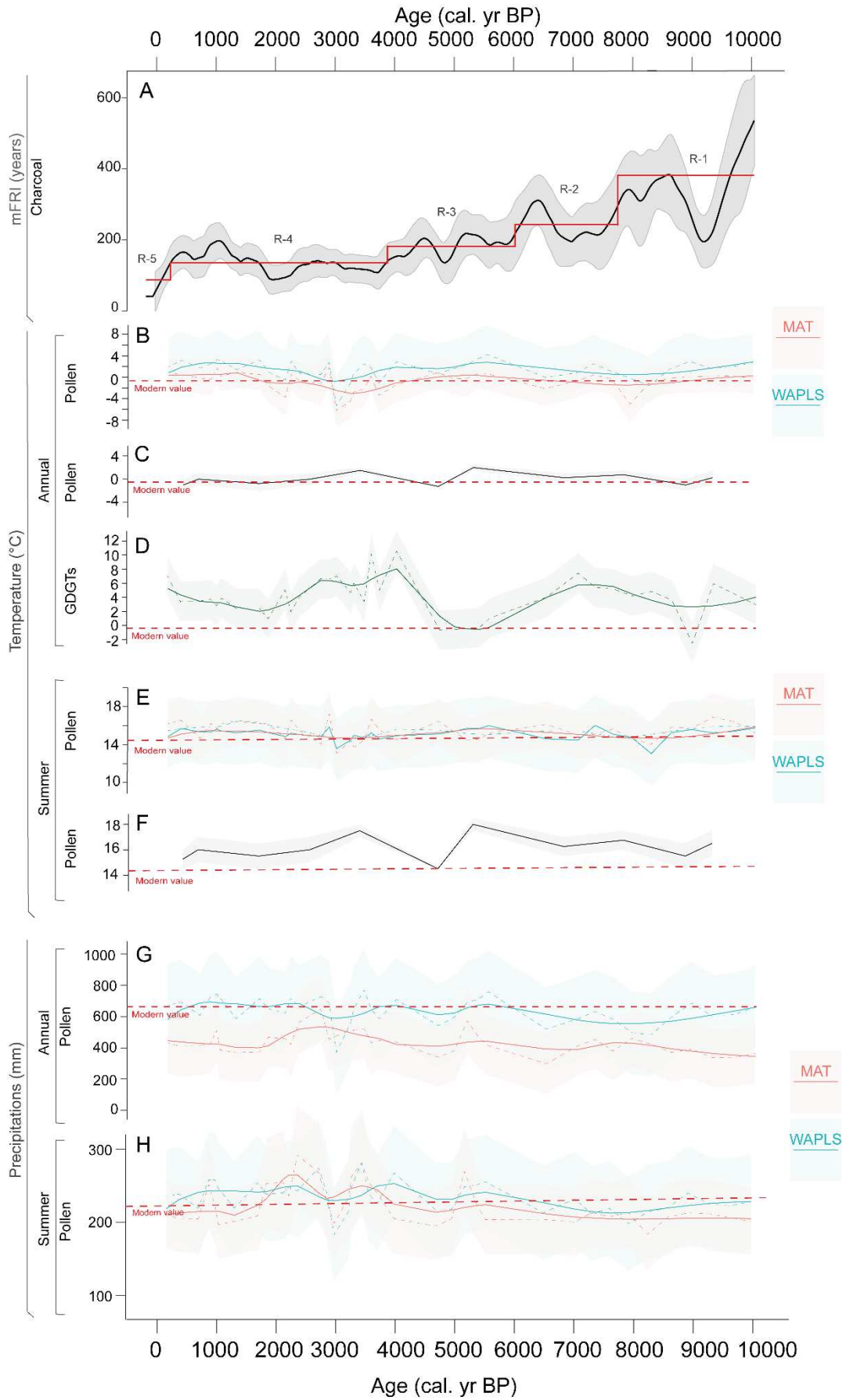
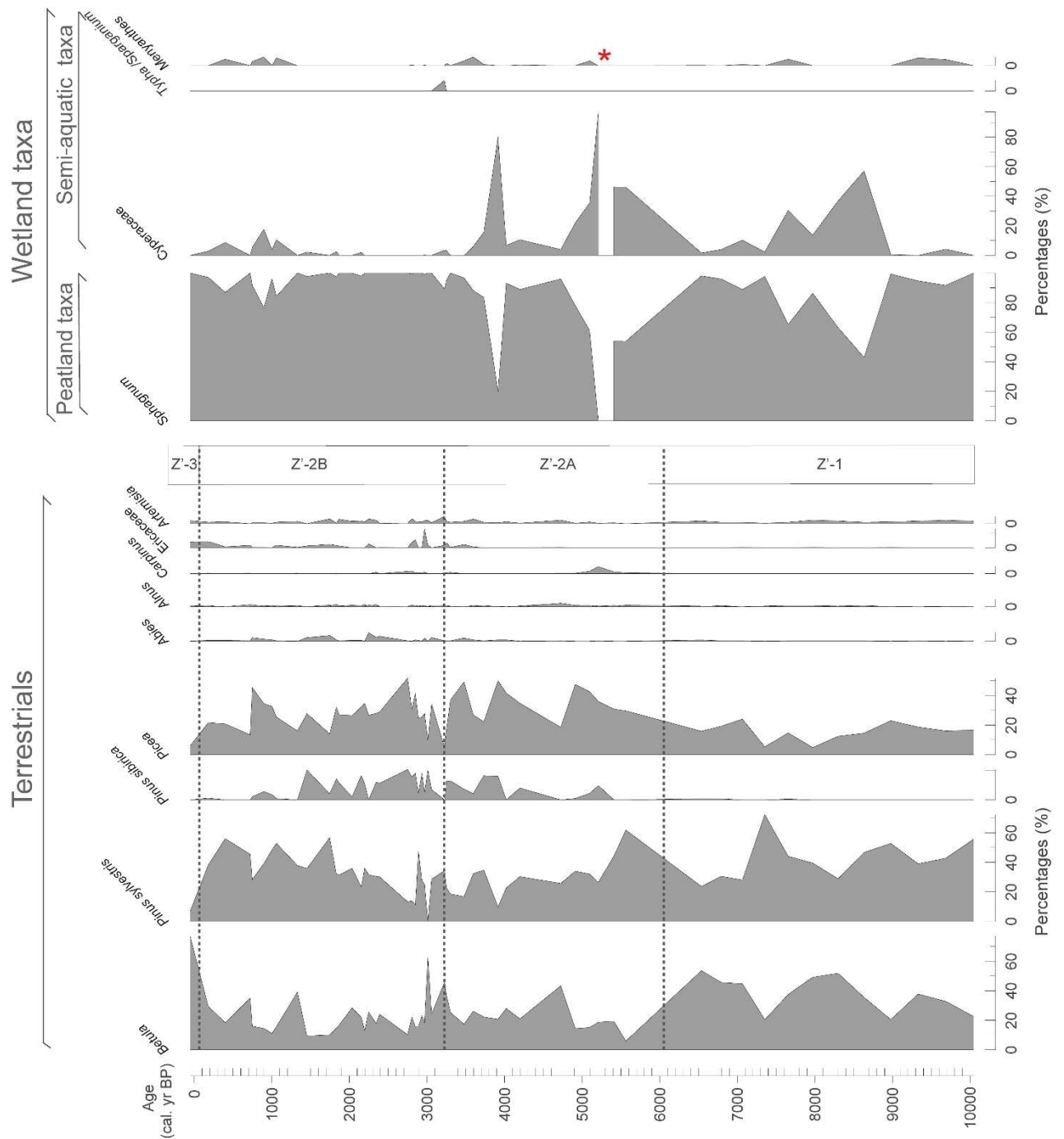


Figure IV.6: Yaksha proxies and comparison with climatic reconstruction from selected locations. (A) mFRI (mean Fire Return Interval) modified from Barhoumi et al., (in press). (B) Pollen-inferred temperature of the mean annual temperature with MAT and WAPLS. (C) Komi Republic mean annual temperature reconstruction from Golubeva, 2008. (D) GDGTs-inferred temperature of the Mean Annual Atmospheric Temperature, from Naafs et al., 2017. (E) Pollen-inferred temperature of the Mean Summer Temperature with MAT and WAPLS. (F) Komi Republic mean July temperature reconstruction from Golubeva, 2008. (G) Pollen-based annual precipitations with MAT and WAPLS. (H) Pollen-based summer precipitations with MAT and WAPLS. Red dashed lines are modern values at Yaksha site.

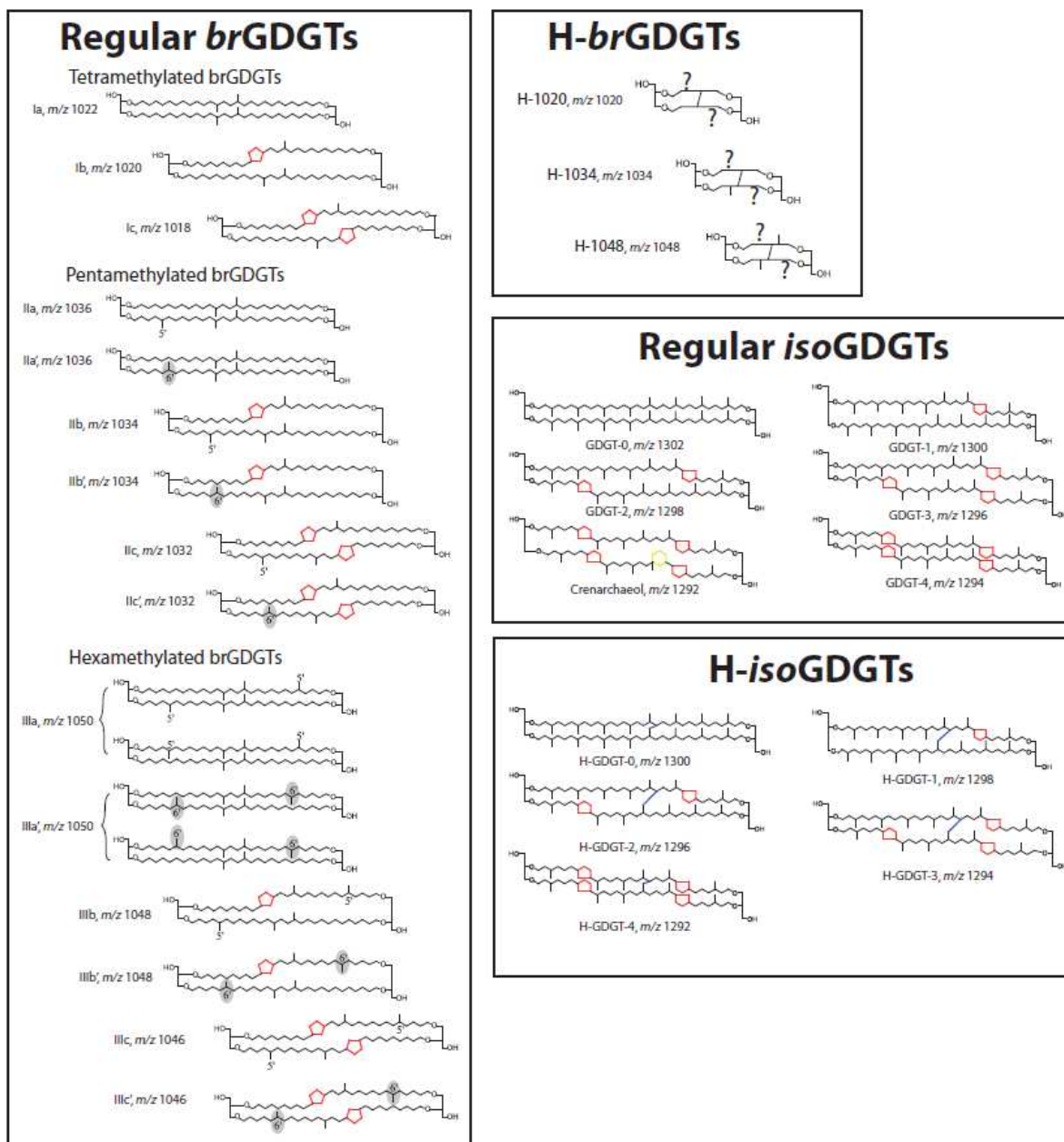
4.6. CONCLUSION

This study highlighted the Holocene climate and the HTM in the Republic of Komi, in the Vychegda River basin, based on current pollen techniques MAT and WAPLS and the study of GDGTs. The results showed that the HTM of the study area is at mid-Holocene, between 7000 and 4000 cal. yr BP. The calibrations obtained by the GDGTs study showed similarities in trends with climate reconstructions from pollen grains study but not temperature values and the HTM was recorded at two periods, between 8500 and 6500 cal. yr BP, then between 4500 and 3000 cal. yr BP . Further studies, including calibrations performed locally at the Yaksha site and regionally in the Republic of Komi, would be necessary to refine the temperature reconstructions performed with the GDGTs study. The relationship between the climatic dynamics of the Republic of Komi and the dynamics of the vegetation and the fire activity will be made in the discussion of the thesis.

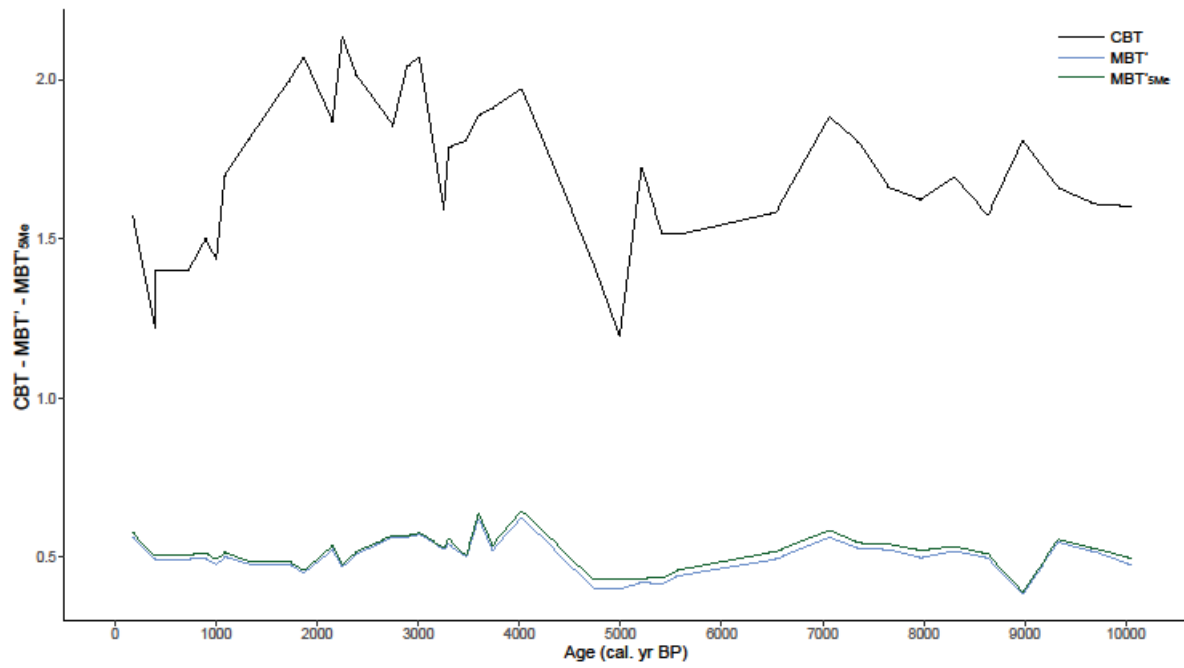
4.7. APPENDICES



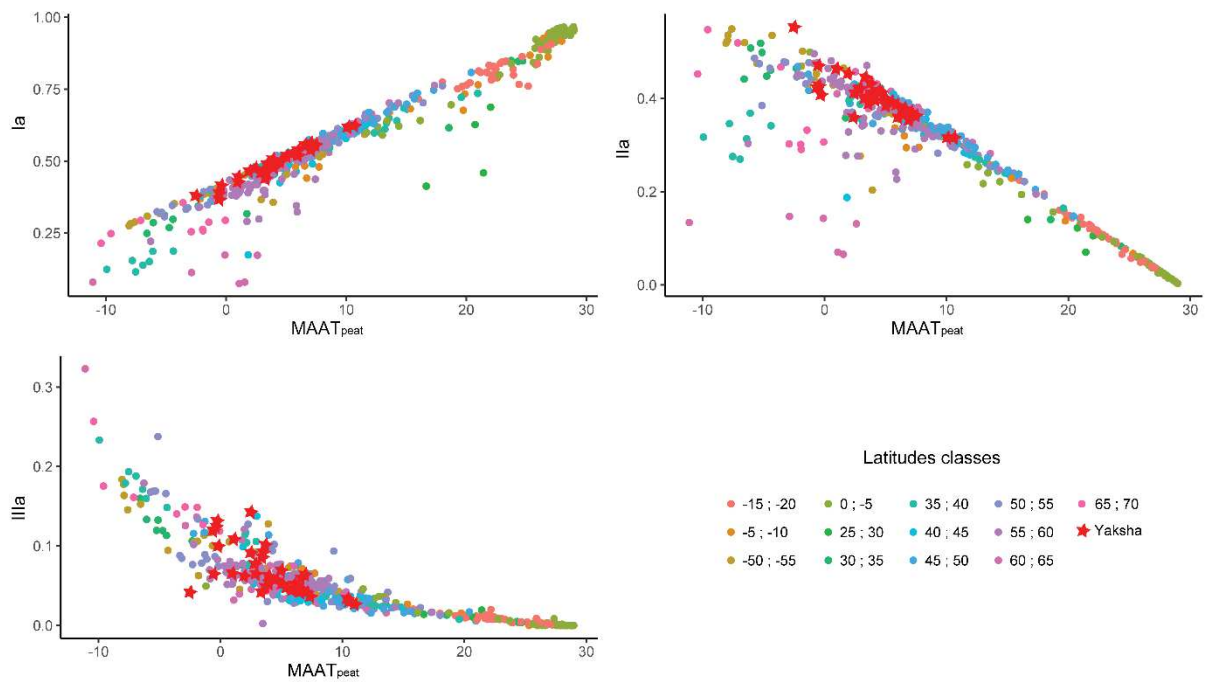
SI 1: Yaksha pollen diagram versus age showing percentages of the main pollen taxa from the Yak2-A and Yak3-A cores, modified from Barhouni et al. (2019). The sample marked with a red star did not contain any Wetland taxa. The pollen diagram was divided into four zones with CONISS: Z'-1 from 10,047 to 6050 cal. yr BP, Z'-2A from 6050 to 3200 cal. yr BP, Z'-2B from 3200 to 60 cal. yr BP and Z'-3 from 60 to -58.



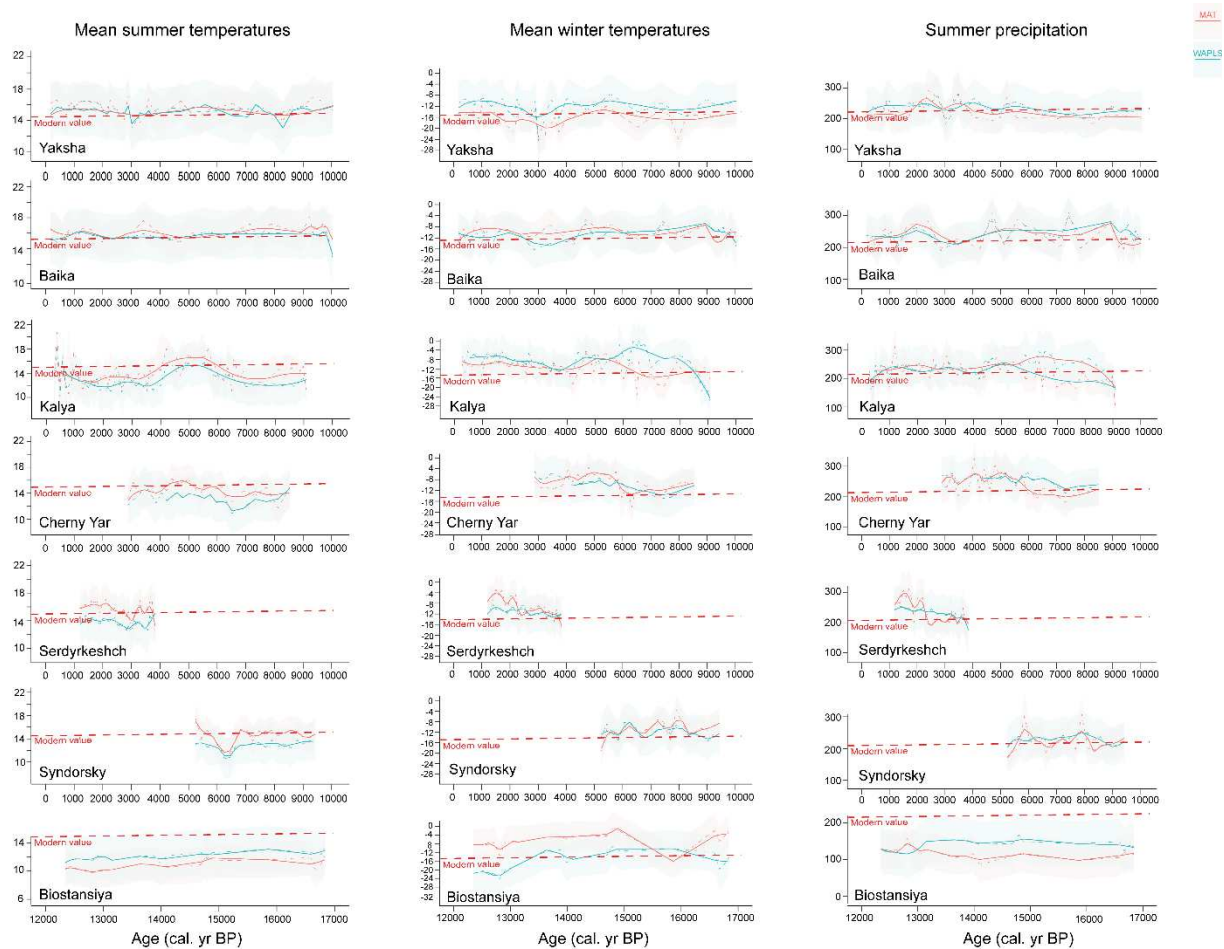
SI 2: Structures of GDGTs discussed in the text. Note that the exact location of the covalent bond between the two alkyl chains in both *Hiso*GDGTs and *H-br*GDGTs is unknown. After Naafs et al., (2018).



SI 3: Yaksha GDGTs indexes CBT, MBT' and MBT'_{5Me}



SI 4: Yaksha GDGTs (Ia, IIa and IIIa against the MAAT_{peat}) compared to the general database from Naafs et al., (2017), sorted by latitude classes



SI 5: Komi Republic pollen-based climatic parameters (Mean summer temperatures, mean winter temperatures and mean summer precipitations) calculated with the modern analogue technique (MAT) and the weighted-average partial least-squares regression (WAPLS) and smoothed with Loess (span = 0.3). Shaded areas are confidence interval.

Chapitre V.

SYNTHESE SUR LES RELATIONS ENTRE LE FEU,
LA VEGETATION ET LE CLIMAT AU COURS DE
L'HOLOCENE EN REPUBLIQUE DE KOMI ET
COMPARAISON DE LA DYNAMIQUE DE FEUX DE
LA CARELIE, LA REPUBLIQUE DE KOMI ET LA
REGION DU LAC BAÏKAL

Les principaux résultats de cette thèse ont montré que l'activité des feux n'a pas été la même tout au long de l'Holocène, en République de Komi (Chapitre II). Le FRI a graduellement diminué, passant d'un intervalle de retour de feu de plus de 400 ans à 10000 cal. yr BP, à un FRI de moins de 100 ans à 0 cal. yr BP. La végétation a également évolué au cours de l'Holocène (Chapitre III) : une taïga claire s'est développée au début de l'Holocène, de 10000 à 6000 cal. yr BP, puis, une taïga sombre s'est progressivement installée de 6000 à 3500 cal. yr BP. Finalement, la taïga claire redevient dominante à partir de 3500 cal. yr BP. Les variations climatiques au cours de l'Holocène en République de Komi sont caractérisées au niveau régional par un optimum thermique entre 7000 et 4000 cal. yr BP, d'après les techniques de quantifications des grains de pollens. Alors qu'avec les calibrations réalisées sur l'analyse des GDGTs, deux périodes d'optimum climatique se sont dégagées, entre 8500 et 6500 cal. yr BP, puis entre 4500 et 3000 cal. yr BP (Chapitre IV). Les températures ont ensuite diminué, avant de remonter pour se stabiliser à partir de 2000 cal. yr BP.

Dans un premier temps, la discussion de cette thèse a pour objectif de comprendre et de discuter les mécanismes qui relient les dynamiques de feux, de végétation et du climat en République de Komi au cours de l'Holocène.

La deuxième partie de cette discussion vise à comparer et discuter la dynamique des feux à une échelle plus large en Russie, à la fois en République de Komi, en Carélie et dans la région du Lac Baïkal pour mieux comprendre les différences et similarités entre signal local et régional et faire émerger des patterns communs, eux-mêmes liés à des processus communs. A l'heure actuelle, il n'y a que très peu d'études visant à retracer l'activité de feux en Russie (Naryshkin, 2003; Lisitsyna et al., 2017).

5.1 INTERACTIONS FEUX-VEGETATION-CLIMAT EN REPUBLIQUE DE KOMI ET FONCTIONNEMENT DE LA FORET BOREALE

La dynamique du facteur feu peut-être interprétée en fonction du facteur climat, mais aussi en fonction du facteur végétation. De même, la dynamique de la végétation peut-être expliquée par celle du climat et celle du feu. Afin de comprendre au mieux les interactions qui relient les incendies, le climat et la végétation en République de Komi, au cours de l'Holocène, et au vu des résultats, la dynamique du facteur végétation va être d'abord interprétée en fonction de la dynamique du climat, pour la première moitié de l'Holocène, puis en fonction de celle du

feu pour la seconde moitié de l'Holocène. Enfin, l'influence de l'Homme sur la végétation et sur la dynamique des incendies sera discutée. Cette démarche se réalise en fonction des différentes phases de végétation établies au chapitre III (de 10000 à 3500 cal. yr BP, de 3500 à 600 cal. yr BP et de 600 à 50 cal. yr BP). Pour ceci, une fonction de densité kernel a été réalisée sur les valeurs des différents paramètres climatiques estimés à partir des six enregistrements polliniques de République de Komi (Chapitre IV), afin de comparer la dynamique de la végétation locale à Yaksha, avec le signal climatique régional (Figure V.1) (Mudelsee et al., 2004).

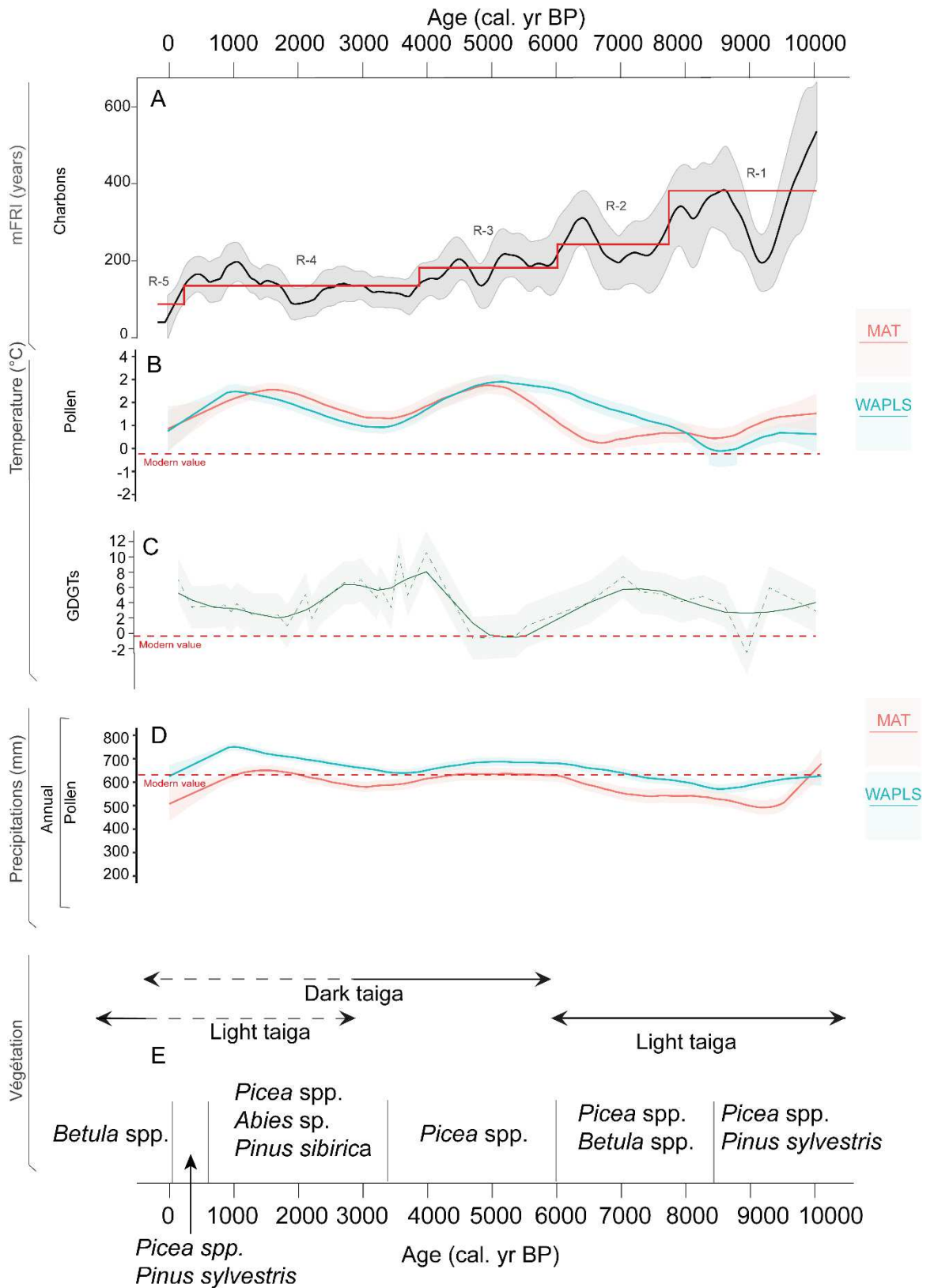


Figure V.1 : Comparaison entre la dynamique des incendies, du climat et de la végétation de Yaksha en République de Komi, au cours de l'Holocène. (A) mFRI, (Barhoumi et al., 2019). (B) Kernel des températures moyennes annuelles estimées à partir des données polliniques (Chapitre IV). (C) Reconstruction des températures à Yaksha, d'après la calibration issue de l'analyse des GDGTs MAAT_{peat}. (D) Kernel des précipitations annuelles estimées à partir des données polliniques (Chapitre IV). (E) Type de forêt boréale et taxon dominant (Chapitre III). Le trait pointillé rouge indique les valeurs moyennes actuelles du site Yaksha.

5.1.1 Climat régional *versus* végétation

Dans la première moitié de l'Holocène, entre 10000 et 6000 cal. yr BP, le climat régional de la République de Komi est caractérisé par des températures et des précipitations proches de l'actuel et par une forêt de type taïga claire (Figure V.1). La présence et l'alternance des taxons *Pinus sylvestris*, *Betula* spp., et *Picea* spp. est cohérente avec l'installation d'une forêt boréale dans cette région depuis 10500 ans cal. yr BP (Golubeva et al., 2008 ; Chapitre III de cette thèse). En effet, les températures et les précipitations étaient bien trop basses au tardiglaciaire pour permettre l'installation de ce type de forêt (Fig IV.2; Golubeva, 2008; Seppä et al., 2009b). Les espèces *Pinus* spp. et *Picea* spp. proviennent de zones refuges plus au sud et de populations installées au-delà de leurs zones optimales de développement (refuges cryptiques), mais qui ont réussi à se développer pendant la période glaciaire avec de faibles densités (Gervais et al., 2002; Giesecke and Bennett, 2004). Le développement de *Picea* spp., provient probablement de deux populations, l'une provenant de la Fennoscandie (*Picea abies*), et l'autre provenant de la Sibérie (*Picea obovata*) (Giesecke and Bennett, 2004; Tollefsrud et al., 2015; Tsuda et al., 2016). De plus, sa localisation aujourd'hui le long des rivières et des cours d'eau, pourrait indiquer que sa migration soit issue de plusieurs petites expansions locales, provenant de corridors écologiques répartis le long du système hydrographique (Zaretskaya et al., 2014).

A la suite de cette période, de 6000 cal. yr BP et jusqu'à 4000 cal. yr BP, le signal climatique reconstruit à l'échelle régionale indiquent un optimum thermique et une augmentation des précipitations (figure V.1). Cet optimum correspond vraisemblablement au HTM mis en évidence auparavant en République de Komi, en Russie arctique et Sibérie, et de manière plus générale, à l'Europe du Nord (Andreev and Klimanov, 2000; Golubeva, 2008;

Seppä et al., 2009a; Tchebakova et al., 2009). Il est toutefois moins marqué par les brGDGTs (Fig V.1C) qui enregistrent une chute des températures entre 7000 et 5500 cal. yr BP à Yaksha. Cette dernière doit vraiment être nuancée par le fait que les GDGTs issues des tourbières des hautes latitudes de l’Hémisphère Nord puissent être plus sensibles aux températures froides (Naafs et al., 2017). De plus, cette baisse de température est bien moins marquée avec les deux autres calibrations testées du Chapitre IV (Figure IV.4). La végétation environnant Yaksha se modifie, premièrement avec *Picea* spp., qui atteint son apogée et caractérise une taïga sombre, puis avec le développement de *Pinus sibirica* et *Abies sibirica* qui renforcent cette taïga sombre. Le réseau hydrographique de ce territoire très peu incliné (pente moyenne de 0.3%) se comble par accumulation sédimentaire (matière organique notamment) tout au long de l’Holocène. Ce phénomène permet l’extension en largeur des zones humides le long de ce réseau, ce qui favorise le développement de *Picea* spp. et de la taïga sombre (Zaretskaya et al., 2014).

De 3500 à 600 cal. yr BP, les précipitations annuelles régionales atteignent leur optimum tandis que les températures annuelles montrent un deuxième optimum avant de diminuer simultanément vers 1000 cal. yr BP pour atteindre des valeurs proches des valeurs actuelles. Ces conditions humides s’accompagnent paradoxalement d’un retour progressif vers une taïga claire, avec l’augmentation de la présence de *Pinus sylvestris*. La taïga sombre ne se résorbe que progressivement. *Picea* spp. est déjà en déclin progressif depuis son optimum vers 6000 cal. yr BP, tandis qu’*Abies* et *Pinus sibirica* ne déclinent qu’à partir de 2500 ans cal. yr BP (Figure III.4). S’il est envisageable qu’*Abies* sp. et *Pinus sibirica* poussaient alors dans le même environnement que *Picea* spp. du fait de leur appartenance à la taïga sombre, le décalage temporel de leur maximum d’abondance ainsi que l’absence des derniers sus-cités aujourd’hui laisse penser que leur milieu de vie au sein de cette forêt boréale était relativement différent de celui de *Picea* spp. En tout état de cause, les conditions climatiques, en particulier les précipitations, restent assez favorables au maintien de la taïga sombre dominante et différent nettement de celles de l’établissement de la taïga claire du début de l’Holocène. Les analyses des GDGTs n’ont pas permis de valider ou non ce pattern des précipitations car leur lien avec ce paramètre climatique n’a pas été établi. La réapparition de la taïga claire ne peut donc pas s’expliquer par le forçage climatique.

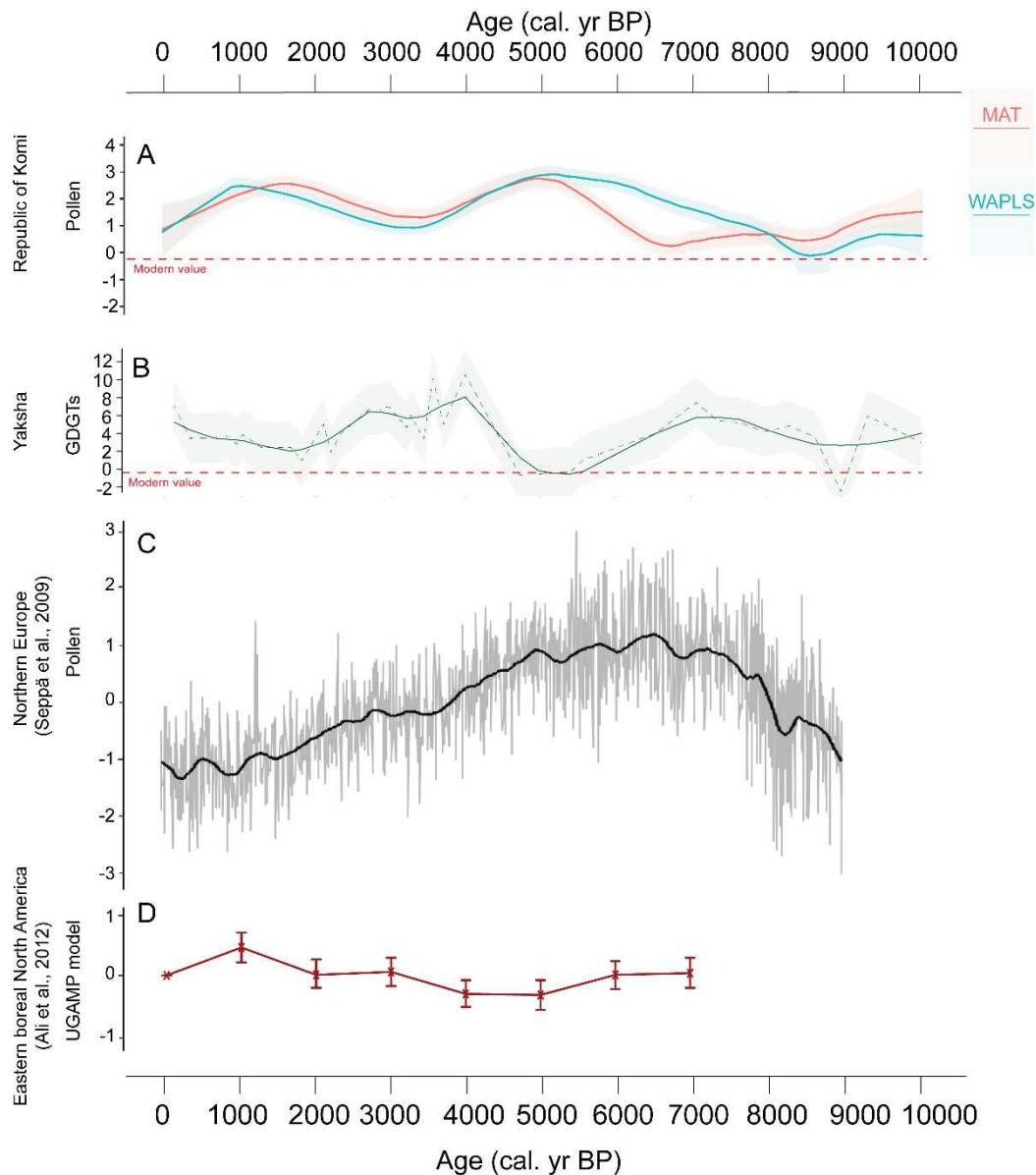


Figure V.2 (A) Kernel des températures moyennes annuelles estimées à partir des données polliniques (Chapitre IV) pour la République de Komi. (B) Reconstruction des températures à Yaksha, d'après la calibration issue de l'analyse des GDGTs $MAAT_{peat}$. (C) Reconstruction des anomalies de températures de l'Europe du Nord à partir des bases de données polliniques, d'après Seppä et al. (2009). (D) Simulation des anomalies de températures du Nord-est boréal de l'Amérique du Nord, issue du model UGAMP, d'après Ali et al., 2012. Le trait pointillé rouge indique les valeurs moyennes actuelles du site Yaksha.

5.1.2. Végétation *versus* feux

Au début de l'Holocène, entre 10000 et 6000 cal. yr BP, (phases de feux correspondantes R-1 et R-2, médianes des mFRI de 350 et 250 ans respectivement), le climat est sec jusqu'à 7000 cal. yr BP, avec des valeurs proches à celles d'aujourd'hui de 7000 à 6000 cal. yr BP. Il est propice au développement des incendies et la présence de la taïga claire pourrait laisser penser que la fréquence des feux y soit élevée (Goldammer and Furyaev, 1996) (Figure V.3). Cependant, la présence importante de *Picea* spp., qui est une espèce qui ne tolère pas le feu et qui ne peut se développer seulement si celui-ci n'est pas fréquent, est en accord avec les valeurs élevées des mFRI enregistrées (Goldammer and Furyaev, 1996). Au cours de cette période, *Picea* spp. est co-dominant avec *Pinus sylvestris* jusqu'à 8500 cal. yr BP, puis avec *Betula* spp. jusqu'à 6000 cal. yr BP. Cette association entre les taxons laisse penser que le paysage était structuré sous forme de mosaïque de taïga sombre et de taïga claire. Une activité de feu de surface pouvait se produire dans la taïga claire, sans atteindre les populations de *Picea* spp.

A partir de 6000 à cal. yr BP, la fréquence des feux continue d'augmenter et la médiane du mFRI est à un peu plus de 200 ans (R-3). Ceci indique une fréquence de feu qui reste faible et compatible avec une végétation d'avantage dominée par la présence de *Picea* spp. (Goldammer and Furyaev, 1996; Schulze et al., 2005; Kuosmanen et al., 2016). Durant cette phase, les feux pourraient avoir été favorisés par l'augmentation des températures annuelles bien que les précipitations estimées soient proches des valeurs actuelles. Cette augmentation des précipitations et de la présence de la taïga sombre pourrait en réalité décrire une densification de la forêt boréale dans laquelle les incendies auraient pu se propager davantage, augmentant ainsi la fréquence d'enregistrement des charbons à Yaksha. D'autres enregistrements de charbons seraient nécessaires pour confirmer ou non cette hypothèse.

Entre 3500 et 600 cal. yr BP, la médiane du mFRI passe sous la valeur seuil à 200 ans (R-4), en même temps que l'augmentation des températures et des précipitations. L'augmentation des précipitations n'est pas toujours associée à une diminution de l'activité de feu, car elle peut d'une part, favoriser la production de biomasse végétale qui fournit le combustible des incendies. D'autre part, des précipitations élevées, mais réparties sur de courtes périodes ont moins d'impact sur l'activité de feu que lorsque les précipitations sont faibles mais continues (Girardin et al., 2006; Bremond et al., 2011). En se basant sur les observations actuelles, ces valeurs de mFRI ne permettent plus à la taïga sombre de se développer

(Goldammer and Furyaev, 1996; Schulze et al., 2005). Le retour progressif à une taïga claire semble donc largement favorisé par la mise en place d'un mFRI plus faible, puisque ce type de forêt est constitué d'espèces tolérantes au feu et bien adaptées à une fréquence des incendies élevés (Goldammer and Furyaev, 1996; Schulze et al., 2005) (Figure V.3). C'est bien cette fréquence de feu qui serait à l'origine des déclinés d'*Abies* sp. et de *Pinus sibirica*, qui ne résistent pas au passage d'un feu et dont la production de graines et le cycle de vie peut être plus long que les valeurs du mFRI de cette phase (jusqu'à 200 ans pour *Pinus sibirica*, Tableau I.1). Pendant cette période, bien que la taïga claire devienne dominante, *Picea* spp. reste cependant bien représenté, probablement toujours en se développant le long des réseaux hydrographiques (Chapitre III). Comme ces réseaux interpénètrent la taïga claire, il est étrange de constater que *Picea* spp. ne souffre pas drastiquement de la baisse du mFRI sous les 200 ans. En théorie, *Picea* spp. ne peut pas se développer si les feux de surface l'atteignent. On peut donc se poser la question de la capacité de ces feux de surface à atteindre les milieux humides tourbeux sur lesquels poussent *Picea* spp., puis à se propager dans un réseau hydrographique sinueux et méandrique de cette région. De plus, ces feux de surface pourraient avoir (en majorité) un caractère extrêmement local, ce qui a pu être mise en évidence dans notre site d'étude par l'analyse des cicatrices de feu sur les arbres. Celle-ci a révélé qu'une majorité de feux ont brûlé certains arbres uniquement, et qu'une minorité ont touché l'ensemble des arbres (Chapitre II, deux incendies en 1861 et en 1936 communs aux trois sites d'études à Yaksha sur les six incendies majeurs détectés). Si les conditions de topographie locale peuvent être la cause de cette disparité (Chapitre II), on peut imaginer que les feux de surface n'arrivent pas à atteindre les populations de *Picea* spp, à cause de leur emplacement sur des zones fortement humides, rendant leur transformation en feu de couronne rare et à propagation limitée.

5.1.3. Le rôle de l'Homme dans la dynamique des relations feu-végétation

La phase 600-0 cal. yr BP montre une taïga claire bien implantée et une dominance de *Betula* sp., qui est une espèce pionnière dans un milieu perturbé et qui est aussi le signe de l'ouverture de la forêt boréale dans cette zone (Goldammer and Furyaev, 1996). Les températures et précipitations correspondent aux valeurs actuelles et le mFRI est le plus bas enregistré à l'échelle de l'Holocène (R-5). Cette phase correspond à la période où l'activité humaine augmente et où la majorité des feux ont une origine humaine (Naryshkin, 2003; Drobyshev et al., 2004a). La très forte présence de *Betula* spp. durant cette phase, associée à un

mFRI si bas, indique un très fort impact humain (feu et coupe). En effet, l'activité humaine dans la région a explosé et depuis le siècle dernier (Chapitre II), l'Homme est devenu la principale cause d'ignition (Naryshkin, 2003; Drobyshev et al., 2004a). En République de Komi en particulier, l'exploitation du bois est une activité très développée et sa production représente une ressource économique majeure pour cette région (Naryshkin, 2003). Ce niveau d'activité de feu pourrait signer une surexploitation de la forêt, dont les espèces conifères déclinent au profit d'une espèce décidue pionnière qui se montre moins affectée par le feu du fait de ses traits écologiques (redémarrage par les racines) ; l'explosion des *Betula* spp. à partir de cette période en est une preuve (Sannikov and Goldammer, 1996; Naryshkin, 2003) Cependant, c'est peut-être la surexploitation des conifères, en particulier celle des pins, par augmentation de la vitesse de rotation des coupes et absence de replantation qui provoque le changement de la composition de la forêt boréale dans cette région (Figure V.3). Ces deux facteurs sont probablement liés et auront pour conséquence probable de fragiliser les secteurs les plus humides à taïga sombre sur tourbière, menant à un renversement de l'équilibre dans le cycle du C, qui se retrouve relargué en masse dans l'atmosphère. Non seulement ces forêts ne tiennent plus le rôle de puits de C comme cela l'a été par le passé, mais deviennent progressivement des sources de C atmosphérique (Naryshkin, 2003; Walker et al., 2019). Avec le réchauffement climatique et la hausse des températures actuelles due à l'activité humaine, les conditions de température et de sécheresse des milieux vont augmenter plus encore, ce qui pourra induire une sécheresse des sols plus importante, permettant ainsi la propagation des feux mêmes sur les zones auparavant humides et donc la combustion plus sévères de populations d'arbres n'étant pas vulnérables auparavant. Ceci a été le cas par exemple dans les années 1972, 1974, 1977, 1982, 1987, 1998 en Sibérie et plus récemment, ces dernières années en Sibérie et dans la région de l'Oural (Goldammer and Furyaev, 1996; Goldammer et al., 2005). La diminution du FRI devrait ainsi encore continuer jusqu'à ce que le climat impacté par les humains ne prennent à nouveau le contrôle de l'histoire du feu par le biais de la diminution de la biomasse forestière. La gestion de la structure des peuplements par l'implantation d'espèces plus adaptées aux nouvelles conditions climatiques locales pourrait avoir un impact contraire sur l'augmentation de l'activité de feu observée aujourd'hui.

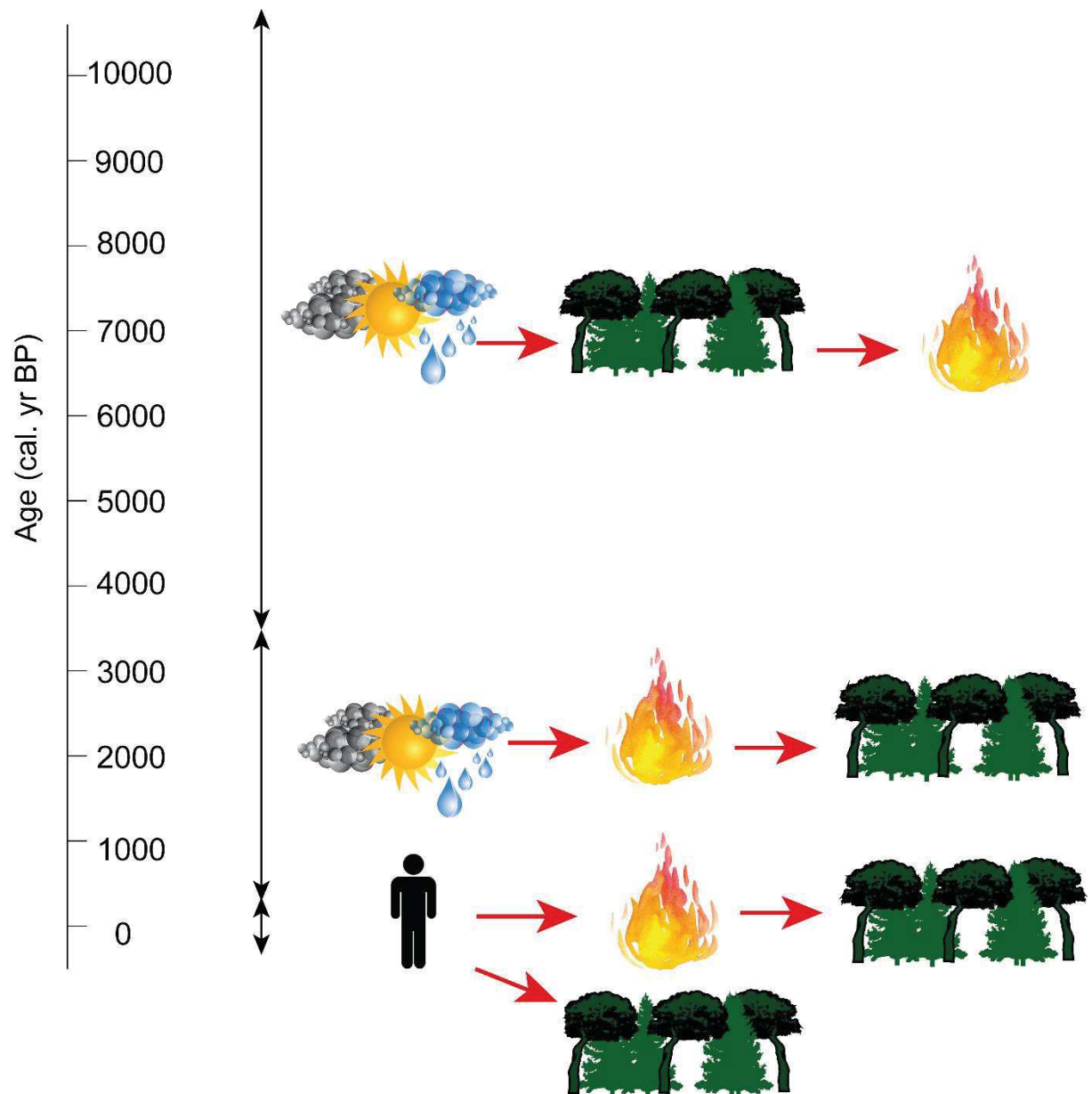


Figure V.3: Impact des facteurs climat, feu et végétation les uns par rapport aux autres, au cours de l'Holocène en République de Komi

5.2. LA DYNAMIQUE DES FEUX DE L'Holocène EN RUSSIE : REPUBLIQUE DE KOMI, CARELIE ET REGION DU LAC BAÏKAL

5.2.1. Variation de la dynamique des feux en Carélie au cours de l'Holocène

Deux lacs ont été étudiés en Carélie : Vohto1 et Vohto2, à une distance de 1 km l'un de l'autre. Ces lacs ont permis d'obtenir des sédiments qui recouvrent des enregistrements allant de 11370 à 4830 cal. yr BP pour Vohto1, et de 21800 à 8350 cal. yr BP pour Vohto2 (modèles d'âge, cf Annexe 1). Ces deux lacs sont situés en forêt boréale, dominée par *Pinus sylvestris/Picea abies* et de *Betula* sp. Seuls les résultats acquis pour l'Holocène (11700 à 4830 cal. yrs BP) seront présentés et discutés dans ce chapitre.

Les résultats montrent que le lac Vohto1 présente un FRI de 80 ans, dès le début de l'Holocène à 11370 cal. yr BP (Figure V.4), FRI qui augmente ensuite à 200 ans jusqu'à 9800 cal. yr BP. Il diminue ensuite à 80 ans jusqu'à 7000 cal. yr BP avant d'augmenter brièvement à 6500 cal. yr BP, à 200 ans, puis diminue à nouveau jusqu'à la fin de l'enregistrement, à 4830 cal. yr BP. Les valeurs de FRI du lac Vohto2 sont supérieures à celles indiquées par Vohto1 : à 12000 cal. yr BP, le FRI de Vohto2 est de plus de 400 ans, puis il augmente à 650 ans jusqu'à 9900 cal. yr BP, puis diminue jusqu'à 250 ans à 8800 cal. yr BP.

Les valeurs de FRI de ces deux lacs ne sont pas similaires, et Vohto2 présente un FRI deux fois plus élevé que celui de Vohto1. La différence dans les valeurs de FRI observée entre les deux lacs est cohérente avec d'autres études de dynamique des incendies dans les régions boréales et en Carélie (Hellberg et al., 2004; Kuosmanen et al., 2014). Ces études montrent que la dynamique des feux peut varier à une échelle locale, entre deux sites, dû à la végétation clairsemée qui se développe dans ce type de forêts et à l'hétérogénéité de la topographie (Kuosmanen et al., 2014). Les deux sites d'études Vohto1 et Vohto2 sont proches géographiquement, cependant, ils se trouvent dans une région riche en lacs et en zones humides. Ceci peut également avoir un fort impact dans la propagation des feux de ces zones, en particulier des feux de surface. Dans ce cas, les conditions locales de topographie, végétation et de microclimat ont pu prévaloir pour expliquer la différence de FRI observée (van Bellen et al., 2012; Kuosmanen et al., 2014). Toutefois on ne peut tester ces paramètres, en particulier la dynamique de la végétation qui n'est pas connue sur le secteur d'étude.

Bien que les valeurs des FRI de ces deux lacs soient différentes, les tendances observées sont similaires entre 12000 et 8800 cal. yr BP, avec une augmentation du FRI, qui indique une diminution de la fréquence des feux au début de l'Holocène, de 12000 à 9800 cal. yr BP, puis une diminution jusqu'à 8800 cal. yr BP. Les faibles valeurs de FRI au début de l'Holocène peuvent être expliquées par le manque de biomasse de végétation à brûler disponible à cette époque, à cause des conditions glaciaires auparavant (Veski et al., 2012; Clear et al., 2014). La diminution du FRI entre 9900 et 7000 cal. yr BP, indiquant une augmentation de la fréquence des feux, est cohérente avec les résultats obtenus par Clear et al. (2014) en Fennoscandie, et peut être expliquée par la mise en place de forêts qui arrivent progressivement sur la zone depuis leur positions refuges donc du carburant disponible au début de l'Holocène, grâce à l'augmentation des températures (Giesecke and Bennett, 2004). De plus, au début de l'Holocène, à partir de 10000 cal. yr BP, un réchauffement a été enregistré en Russie arctique, par Andreev et Klimanov (2000), ce qui a pu contribuer à une augmentation de l'activité de feu en Carélie, à cette période (avec une nette diminution du FRI). Des études de dynamique des incendies en Fennoscandie ont montré que de manière générale, l'activité des feux était plus élevée entre 7500 et 4500 cal. yr BP, principalement liée à des conditions de réchauffement climatique et de conditions sèches, propices aux feux dans cette région (Figure V.2) (Tarasov et al., 1999; Carcaillet et al., 2007; Seppä et al., 2009a; Kuosmanen et al., 2014).

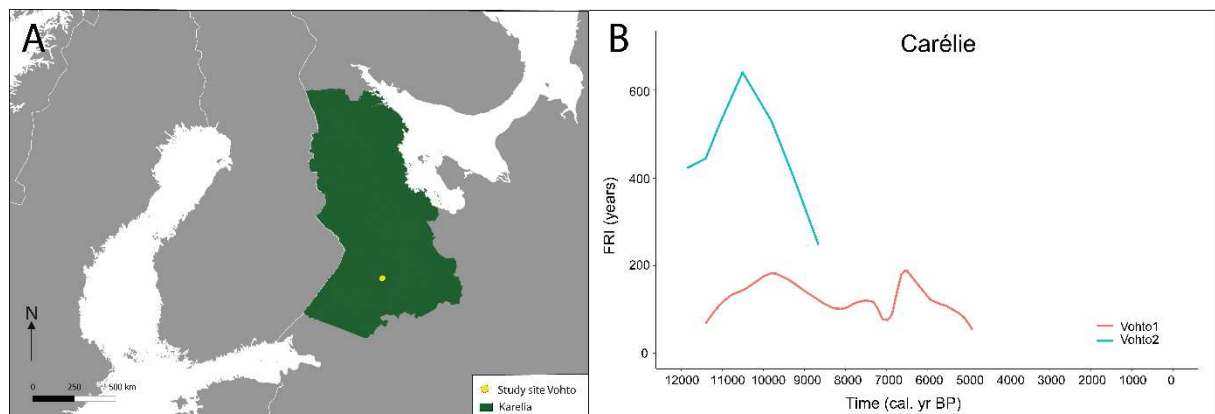


Figure V.4:A. Carte de la Carélie et du site d'étude montrant les deux lacs « Vohto ». B. FRI calculé pour la première moitié de l'Holocène, à partir des deux lacs étudiés, Vohto1 et Vohto2.

5.2.2. Variations de la dynamique des feux dans la région du Lac Baïkal au cours de l'Holocène

Deux lacs ont été étudiés dans le sud du Lac Baïkal : les lacs « Ébène » et « Jarod ». Ils sont situés à une distance d'environ 4 km l'un de l'autre et l'autre et enregistrent tous les deux la période Holocène dans sa totalité (Annexe 2). Ces lacs sont entourés de forêts composées majoritairement de *Pinus sylvestris*, *Betula* spp., *Picea obovata*, *Pinus sibirica* et *Abies sibirica* (taïga claire et sombre co-dominante). Actuellement, le climat de Sibérie est soumis à l'influence de l'anticyclone de Sibérie (SH), qui est caractérisé par des masses d'air froides denses dont l'intensité et l'extension dépendent d'anomalies de chaleur associées au couvert neigeux des régions au-dessus desquelles il agit (Cohen et al., 2001).

Les dynamiques des feux entre ces deux lacs sont similaires et indiquent des périodes d'augmentation ou de diminution des feux qui sont communes (Figure V.5). Le début de l'Holocène est marqué par une augmentation du FRI de 11000 à environ 9200 cal. yr BP, puis une diminution du FRI jusqu'à environ 8500 cal. yr BP. Une autre diminution est enregistrée de 8500 à 5500 cal. yr BP, suivi d'une augmentation jusqu'à 4500 cal. yr BP. Pour le lac Jarod, le FRI diminue ensuite jusqu'à la fin de l'enregistrement alors que pour le lac Ébène, une augmentation a lieu entre 2800 et 1500 cal. yr BP. L'augmentation du FRI du début de l'Holocène a lieu en même temps que l'apparition de la taïga sombre, composée d'espèces non résistantes au feu et donc adaptées à une fréquence faible des incendies, telles que *Pinus sibirica* et *Abies sibirica* (Demske et al., 2005). Puis, de 9200 à environ 7000 cal. yr BP, le FRI diminue, ce qui indique peut-être le rôle de la biomasse disponible dans la dynamique des feux, puisque celle-ci est à son maximum à cette époque. Ensuite, de 7000 à 5500 cal. yr BP, la région connaît son optimum climatique, et une augmentation de *Pinus sylvestris*, ce qui peut expliquer les diminutions du FRI observées (Bezrukova et al., 2013). L'augmentation du FRI qui suit (jusqu'à 4500 cal. yr BP) peut être associée à un refroidissement marquant la fin du HTM de cette région (Bezrukova et al., 2013). Lorsque le FRI diminue à nouveau, de 4500 à 2500 cal. yr BP, la forêt de *Pinus sylvestris* devient co-dominante et ces deux facteurs peuvent avoir été impliqués dans une dynamique commune (Demske et al., 2005; Bezrukova et al., 2013). Une augmentation du FRI a ensuite lieu de 2500 à 1500 cal. yr BP, en phase avec l'augmentation des conditions humides à l'échelle régionale (Demske et al., 2005; Bezrukova et al., 2013). Finalement, les

derniers 1500 ans sont marqués par une diminution constante du FRI, et donc une augmentation de l'activité des feux, ce qui pourrait être en partie liée à l'augmentation de l'impact humain dans cette région (Tarasov et al., 2007).

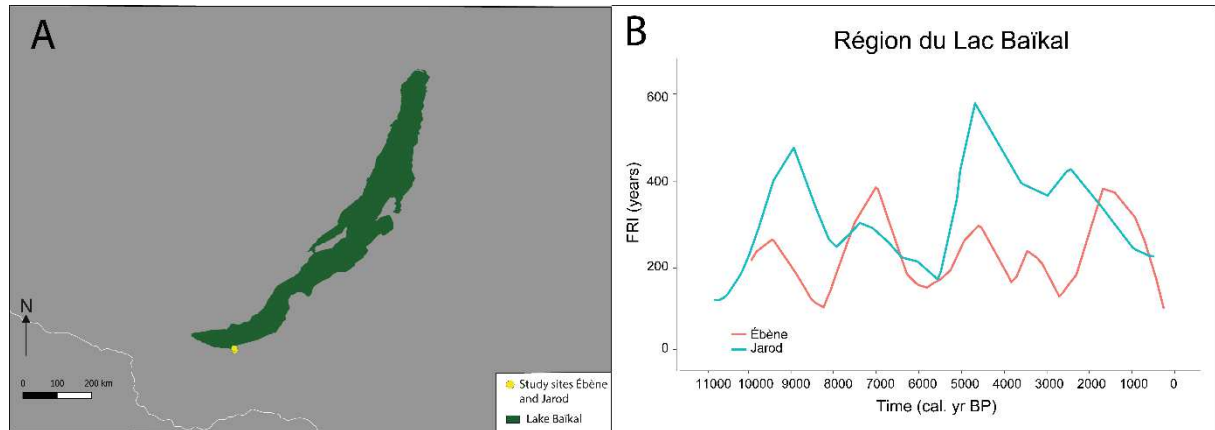


Figure V.5 : A. Carte de la région du Lac Baïkal et localisation des lacs « Ébène » et « Jarod ». B. Reconstitution du FRI des deux lacs Ébène et Jarod, au cours de l'Holocène.

5.2.3. Variations de la dynamique des feux en Russie au cours de l'Holocène et comparaison aux autres régions boréales

La dynamique des feux au cours de l'Holocène a varié en fonction des régions étudiées (Figure V.6). Le FRI a été en constante diminution en République de Komi, alors qu'il a évolué de façon plus complexe en Carélie et dans la région sud du Lac Baïkal (Figure V.6). Aujourd'hui, 80% des feux qui brûlent en Eurasie (et donc en Russie) sont des feux de surface, qui sont adaptés à la présence de taïga claire (Sannikov and Goldammer, 1996). Ce sont des feux de faible intensité, qui ne sont en général pas délétères aux arbres qu'ils touchent, étant au contraire bénéfiques à leur développement (ex : *Pinus sylvestris*, *Betula* sp., *Larix* sp.) (Sannikov and Goldammer, 1996; Schulze et al., 2005). Au Canada, au contraire, les feux de forêts sont majoritairement des feux de couronne et détruisent les arbres lorsqu'ils se produisent (Sannikov and Goldammer, 1996). L'étude du FRI des différentes régions étudiées permet de connaître la fréquence des feux mais ne permet pas de déterminer leur sévérité et leur nature (feux de surface ou de couronne). Cette information pourrait être utile pour approfondir la compréhension de la dynamique des feux dans ces régions. En revanche, pour discuter du type d'incendie, on peut s'attacher à analyser les nuances qui s'expriment à l'intérieur de la Russie

aujourd'hui. La majorité des feux qui brûlent en République de Komi et en Carélie sont des feux de surface, alors que dans la région du lac Baïkal, les deux types d'incendies se produisent (Sannikov and Goldammer, 1996; Naryshkin, 2003; Schulze et al., 2005; Kuosmanen et al., 2014). L'étude complète menée en Komi a permis de constater que le seuil FRI = 200 ans avait entraîné sur les 3500 dernières années la transformation de la végétation au profit de forêt d'espèces adaptées aux fréquents feux de surface. A l'inverse, les périodes de l'Holocène où le FRI fût élevé (supérieur à 200 ans) pourraient indiquer une production de feux de couronne plus importante que les feux de surface et notamment lorsqu'une forêt de type taïga sombre est elle-même dominante à co-dominante. Ce seuil à 200 ans semble aussi s'établir sur la partie la plus récente de l'enregistrement de Carélie (i.e. 4500 cal. yr BP). Toutefois ici le manque de l'intervalle récent faisant le lien avec l'actuel, ainsi que l'absence de données de végétation ne permettent pas de tester la validité de ce seuil. L'étude de l'activité de feu dans la région du Lac Baïkal montre un patron fluctuant autour de ce seuil qui peut être associé à la codominance elle-même fluctuante de taïga sombre et claire (Bezrukova et al., 2013). Malgré l'hétérogénéité du jeu de données de cette comparaison, les FRI indiqués par les études du passé (inférieurs à 200 ans en Komi depuis 3500 ans, fluctuant autour de 200 ans au Baïkal) correspondent aux types de feux constatés actuellement. Cela questionne d'autant l'impact des humains sur la végétation et la fréquence des feux.

En République de Komi et dans la région du Lac Baïkal, une nette diminution du FRI est observée à la fin de l'Holocène, depuis environ 1000 ans. Dans les deux régions, l'augmentation de l'activité humaine est mise en cause dans ce processus : en République de Komi, plus de 65% des feux sont allumés par les hommes, de manière accidentelle et en Sibérie, l'impact des populations humaines sur les feux de forêts a augmenté à travers un manque de contrôle et une politique de gestion des feux très controversée (Naryshkin, 2003; Mollicone et al., 2006). Aujourd'hui, l'impact humain sur les feux s'exerce à la fois en tant que source d'ignition principale, mais aussi à travers le réchauffement climatique et l'augmentation des conditions de sécheresse, ce qui mène à des feux de forêts plus fréquents, mais aussi plus sévères (de Groot et al., 2013; Walker et al., 2019). L'augmentation dans la fréquence des feux est en train de modifier le cycle du C associé à ces forêts et dans la mesure où les jeunes forêts, qui sont historiquement des puits de C deviennent de plus en plus vulnérables aux feux, l'impact des feux de forêts pourraient y modifier l'équilibre du C et les transformer en source de C (Walker et al., 2019).

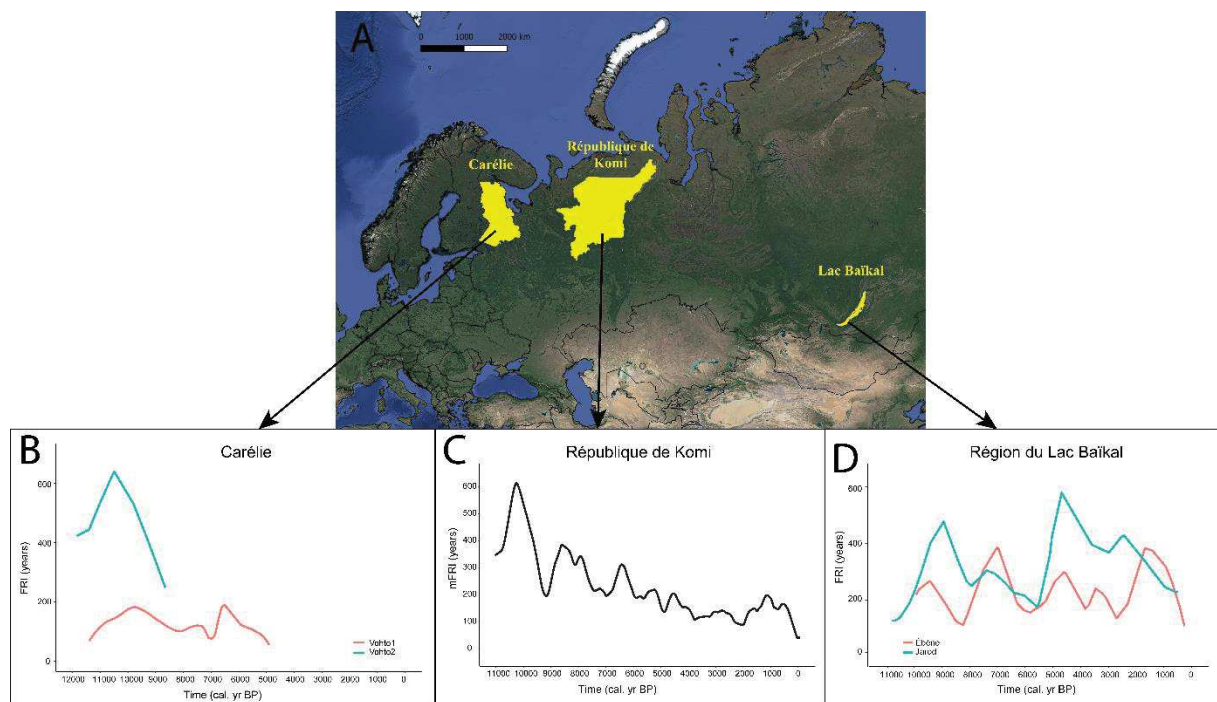


Figure V.6 : A. Carte des 3 régions étudiées en Russie. B. FRI de la première moitié de l'Holocène, des deux lacs étudiés en Carélie, Vohto1 et Vohto2. C. mFRI de la République de Komi au cours de l'Holocène. D. FRI des deux lacs étudiés Ébène et Jarod, au cours de l'Holocène.

La dynamique des incendies reconstruite dans cette étude est à mettre en relation avec les tendances climatiques générales qui ont été bien documentées et établies au Canada et en Europe du Nord notamment (Girardin et al., 2006; Ali et al., 2009a; Hély et al., 2010; Ali et al., 2012; Drobyshev et al., 2016). Au Canada de l'Est, l'étude de la dynamique des incendies a révélé une activité de feu peu développée, comme en République de Komi, entre 8000 et 5800 cal. yr BP, mais les conditions climatiques favorables qui sont apparues à partir de 5800 cal. yr BP ont permis l'augmentation de la fréquence des feux. Alors qu'à partir de 4000 cal. yr BP, les facteurs écologiques locaux ont pris plus d'importance dans le contrôle du feu que le climat (Ali et al., 2009a). Le climat canadien, associé au contrôle des incendies, dépend largement de grands systèmes bloquants à haute pression (pression atmosphérique à 500 hPa) qui se produisent au-dessus de la région (Girardin et al., 2006). L'arrêt de ces blocages induit une activité de convection, qui est la source de nombreux orages et éclairs, qui démarrent les

incendies. Depuis les années 1850 AD, la fréquence des feux a diminué au Canada, en partie à cause des conditions d'humidité qui ont augmenté (Girardin et al., 2006). Les liens actuels entre la circulation atmosphérique et la dynamique des incendies laissent supposer que les changements passés des régimes de feu étaient également soumis à des changements dans la circulation des masses d'air et des températures de surface des océans (Girardin et al., 2006). Ainsi, deux composantes de circulation atmosphérique opèrent au Canada : une circulation de vents d'ouest froids et humides pendant les années avec peu de sécheresse, mais une circulation de vents du nord froids et secs, pendant les années de sécheresse sévère (Girardin et al., 2006). Ces circulations de vents sont liées aux anomalies de température de surface des océans, au niveau de l'Arctique, du Pacifique (El Nino) et de l'Atlantique (Oscillation de l'Atlantique du Nord, NAO) (Ali et al., 2009a). L'augmentation de l'activité de feu à partir de 5800 cal. yr BP, serait en partie dûe aux anomalies des températures de surface des océans pacifiques et atlantiques, qui auraient permis la venue de masses d'air sèches arctiques, alors que sa diminution à partir de 4000 cal. yr BP, serait liée au changement climatique du Neoglaciale (Figure V.2), correspondant à un climat plus froid et plus humide, dû à une invasion de masses d'air froides et humides depuis les zones tropicales humides (Ali et al., 2009a).

En Fennoscandie également, des processus climatiques à large échelle ont eu un impact sur l'activité des feux. Ainsi, des anomalies de températures des océans (NAO) chaudes ont générés des conditions de sécheresse, alors que des anomalies de températures des océans froides ont provoqués des conditions plus humides (Seppä et al., 2009a). Entre 8000 et 5000 cal. yr BP, les conditions climatiques chaudes et sèches ne seraient pas uniquement dûes à l'augmentation de l'insolation, mais elles auraient aussi été mises en place grâce à une circulation anticyclonique en été (Seppä et al., 2009a). En Suède, Drobyshev et al. (2012) ont montré que la dynamique de l'activité de feu entre le 19^{ème} et le 20^{ème} siècle était liée aux phases de la NAO, avec une phase négative entraînant une diminution de l'activité cyclonique sur le nord-ouest de l'Europe et associée à des anomalies de précipitations négatives, entraînant une diminution de la teneur en eau des combustibles forestiers et, par conséquent, un risque d'incendie accru. Drobyshev et al. (2016) ont également montré l'influence des anomalies de températures océaniques de l'Atlantique sur l'activité des feux en Suède. Ainsi, ils ont proposé que les conditions de températures froides sur le nord de l'Atlantique Nord, associées à de faibles anomalies, redirigent vers le sud les précipitations associées aux vents d'ouest et entraînent une activité accrue des feux régionaux. Ils ont également supposés que ces éléments de contrôle ont pu opérer à différentes échelles de temps pendant l'Holocène.

Ces résultats laissent à penser que l'influence climatique sur l'activité de feu enregistrée en République de Komi, en Carélie et dans la région Sud du Lac Baïkal serait également liée à des processus de circulations des masses d'airs et des courants océaniques.

La République de Komi correspond à une zone particulière en termes de climat, au confluent entre l'AO provenant du Nord, la NAO provenant de l'ouest et le SH provenant de l'est (Han et al., 2011). Cette région est également sous l'influence du blocage de l'Oural (UB) dont l'intensité dépend des phases de l'AO et du NAO (Cheung and Zhou, 2015b; Gong and Luo, 2017; Luo et al., 2017). En République de Komi, qui est au niveau du versant ouest de l'Oural, les phases positives du NAO/AO seraient favorables à une activité de feu, tout comme en Scandinavie, car elles permettraient de réduire l'impact froid du SH par le renforcement de l'UB, qui bloquerait le passage d'air froid en provenance de l'est (Cheung and Zhou, 2015b; Drobyshev et al., 2016).

Ces interactions très complexes entre les différents systèmes de hautes pressions de circulation atmosphériques sont peu documentées dans les zones d'étude, contrairement à l'Amérique du Nord, et le rôle qu'ils tiennent par rapport à l'activité des feux passés demeure peu connu (Girardin et al., 2006; Ali et al., 2009a; Drobyshev et al., 2016)

5.3. CONCLUSIONS ET PERSPECTIVES

Cette thèse constitue une des premières études multi-proxies pollen-charbons-biomarqueurs moléculaires pour la période de l'Holocène en Russie. Elle combine à la fois des analyses de charbons lacustres pour l'étude des feux passés, des analyses polliniques et l'utilisation du modèle REVEALS pour retracer les changements de végétation, et des fonctions de transferts et biomarqueurs moléculaires de type brGDGTs pour quantifier les paleoclimats. C'est également une des premières études qui effectue la comparaison entre les reconstructions climatiques provenant de l'analyse des séries pollens, avec la reconstitution effectuée par les GDGTs, qui est un proxy très récent et en cours de développement.

La Russie est un territoire vaste et l'étude d'autres zones, à la fois en République de Komi (au Nord par exemple) et à la fois dans d'autres régions (en Sibérie du Nord, de l'Est, au niveau du Sud de l'Oural etc.) est nécessaire pour comprendre les subtilités des mécanismes qui régissent les dynamiques feu-végétation-climat qui s'y déroulent. Les méthodes utilisées pour répondre aux objectifs de la thèse, comme par exemple l'utilisation des brGDGTs pour la

reconstruction des températures passées, doit être perfectionnée et des calibrations adaptés aux sites d'études sont à réaliser. La reconstruction des fréquences de feux *via* les FRI doit aussi s'accompagner de la reconstruction de la sévérité de ceux-ci afin d'obtenir des informations plus précises sur les dynamiques des feux passés.

D'autres processus écologiques sont également à étudier et à coupler avec l'étude des feux pour améliorer la compréhension de la dynamique passée et actuelle, mais aussi permettre d'améliorer les projections futures du fonctionnement des forêts boréales. Parmi ces processus, d'autres perturbateurs des forêts boréales demeurent peu documentée en Russe. C'est le cas en ce qui concerne les épidémies d'insectes ravageurs et de champignons (Gromtsev, 2002). Les infestations d'insectes peuvent provoquer des pertes de bois considérables et ont un impact significatif sur l'équilibre du C dans les forêts boréales. De plus, la quantité d'arbre touchés par ces infestations peut représenter le double de ce qui est provoqué par les incendies annuellement (McCullough et al., 1998; Volney and Fleming, 2000). Ces perturbateurs représentent donc un élément majeur dans la dynamique des forêts boréales mais leur préservation est rare dans les archives sédimentaires. Dans le contexte du changement climatique actuel, il prend de l'importance puisque les éclosions et le cycle de vie de ces insectes dépendent directement des conditions climatiques et météorologiques de leur habitat (Volney and Fleming, 2000).

L'étude du rôle des tempêtes dans la mise en place des châblis est un autre élément à prendre en compte, notamment pour la compréhension de la structure des paysages en mosaïque dans les forêts boréales, en lien avec le réseau hydrographique par exemple (Gromtsev, 2002). Les différentes espèces qui composent la forêt boréale ne réagissent pas de la même façon après un évènement de type châblis et cet élément pourrait être mis en avant dans la compréhension de l'observation de mosaïques de taïga claire et sombre par le passé.

L'étude de l'impact de la mégafaune sur la dynamique de la forêt, et notamment *via* le processus de broutage, pourrait également se révéler complémentaire à celle des châblis, et associée aux particularités écologiques des espèces qui constituent les forêts boréales, elle pourrait permettre de mieux comprendre la structure complexe de cet écosystème, y compris par le passé (Suominen, 1999; Gromtsev, 2002; Hofgaard et al., 2010).

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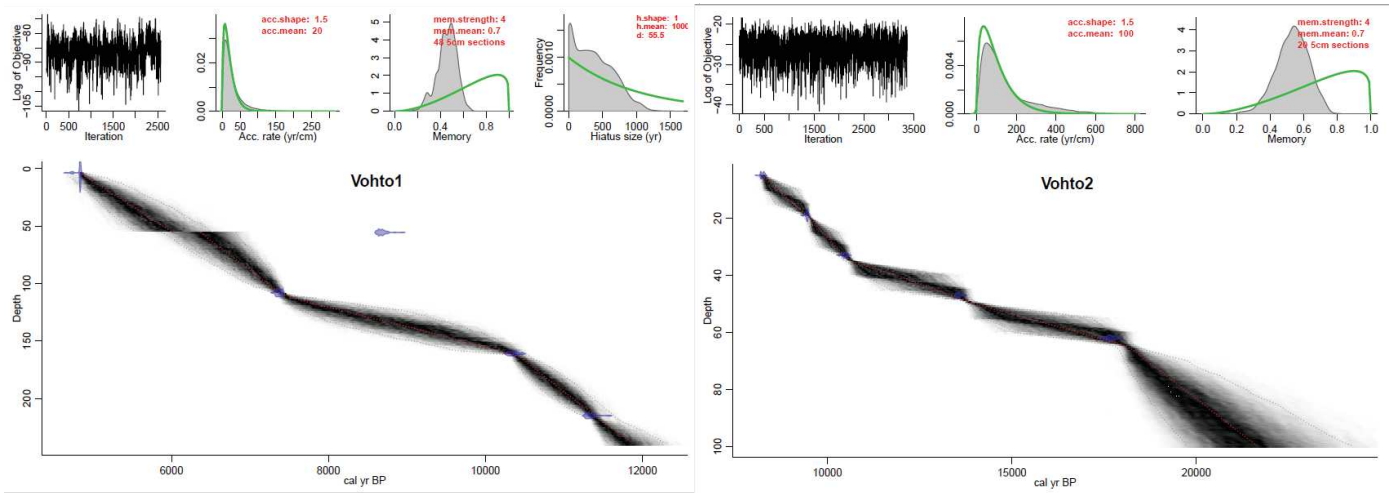
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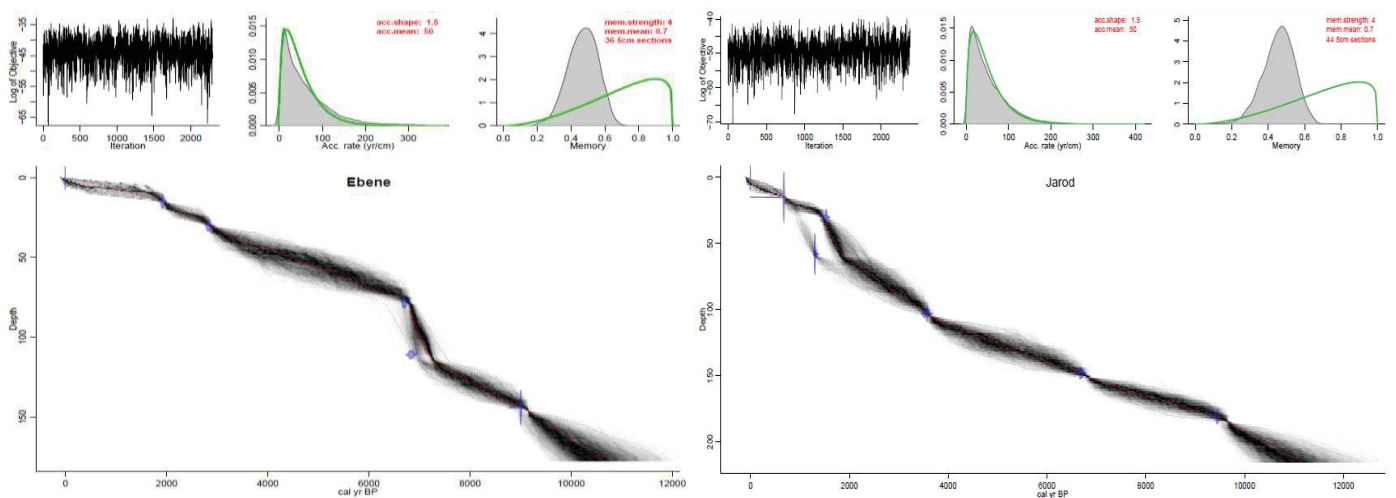
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ANNEXES



Annexe 1 : Modèles d'âge obtenus avec Winbacon, de Vohto1 et Vohto2



Annexe 2 : Modèles d'âge obtenus avec Winbacon, de Èbène et Jardod

Histoire des feux, dynamique de la végétation et variabilité climatique de l'Holocène en République de Komi

Thèse présentée par Chéïma Barhoumi

Encadrée par Odile Peyron, Adam A. Ali et Sébastien Joannin

RESUME

Le changement climatique en cours entraîne et va continuer d'entraîner d'importantes modifications au niveau de la structuration et de la biodiversité des écosystèmes forestiers. Les forêts boréales, qui comptent parmi les plus grands biomes forestiers de la planète (32% du couvert forestier mondiale), sont particulièrement impactées par de tels changements. Les incendies y sont des perturbateurs écologiques majeurs et participent à la dynamique de ces forêts. Afin de mieux comprendre les mécanismes sous-jacents au fonctionnement de cet écosystème, et afin de mieux anticiper les changements encore à venir, l'étude de sa dynamique passée permet d'apporter des éléments de réponses en ce qui concerne les interactions feu-végétation-climat. L'objectif de la thèse consiste à étudier et à comprendre les interactions entre la dynamique des incendies, de la végétation et du climat de l'Holocène (derniers 11700 ans) en République de Komi, une région de Russie, où ces questions ont été très peu documentées. Dans un premier temps, l'étude de la dynamique des incendies a révélé que la fréquence de feu a augmenté de manière graduelle tout au long de l'Holocène. Les changements de végétation au cours de l'Holocène ont été retracés à partir de l'analyse des grains de pollen et du modèle REVEALS. Une forêt de type taïga claire (type particulier de forêt boréale) s'est développée au début de l'Holocène, de 10000 à 6000 cal. yr BP. Ensuite, de 6000 à 3500 cal. yr BP, une taïga sombre s'est installée. Puis à partir de 3500 cal. yr BP, on observe le retour progressif de la taïga claire. Les reconstitutions paléoclimatiques basées sur une double approche, *via* l'étude des grains de pollen et des biomarqueurs moléculaires branched Glycerol Dialkyl Glycerol Tetraethers (brGDGs), ont mis en évidence un optimum climatique entre 7000 et 4000 cal. yr BP. La mise en relation de ces résultats les uns avec les autres nous a amené à conclure que pour la première moitié de l'Holocène, le climat a eu une influence majeure sur la végétation. Puis à partir de 3500 cal. yr BP, le passage de la fréquence des feux sous une valeur seuil (FRI, Intervalle de retour de feu < 200 ans) a eu un impact plus fort que le climat sur la végétation. Depuis les 600 dernières années, l'intensification des activités humaines a mené à une surexploitation de la forêt et à une augmentation de son activité de feu. Un autre aspect de la thèse a consisté à étudier les dynamiques des incendies de deux autres régions, en Carélie et dans la région sud du Lac Baïkal. La dynamique des feux y a été plus complexe qu'en République de Komi, car elle n'a pas suivie la même tendance de décroissance graduelle et continue du FRI.

ABSTRACT

Ongoing climate change is causing and will continue to cause significant changes in the structure and biodiversity of forest ecosystems. Boreal forests, which are among the world's largest forest biomes (32% of the world's forest cover), are particularly affected by such changes. Fires are major perturbators and contribute to the dynamics of these forests. In order to better understand the mechanisms underlying the functioning of this type of forest, and to anticipate future changes, the study of its past dynamics allows us to provide some answers. The aim of this PhD is to study and understand the interactions between the dynamics of Holocene fire, vegetation and climate (last 11700 years) in the Republic of Komi, a region of Russia, where these questions have been very poorly documented. Vegetation dynamics during the Holocene were reconstructed from pollen grain analysis and the REVEALS model. A light taiga forest (a particular type of boreal forest) developed in the early Holocene, from 10,000 to 6,000 cal. yr BP. Then, from 6000 to 3500 cal. yr BP, a dark taiga settled. Then from 3500 cal. yr BP, we observe the gradual return of the light taiga. Paleoclimatic reconstructions based on a dual approach, pollen grains and molecular biomarkers branched Glycerol Dialkyl Glycerol Tetraethers (brGDGs) studies, have shown a climatic optimum between 7000 and 4000 cal. yr BP. The relationship between these results led us to conclude that for the first half of the Holocene, climate had a major influence on vegetation. Then from 3500 cal. yr BP, the change in fire frequency below a threshold value (FRI, Fire Return Interval < 200 years) had a greater impact on vegetation than the climate. Over the past 600 years, the intensification of human activities led to overexploitation of the forest and an increase in its fire activity. Another aspect of the PhD was the study of the fire dynamics of two other regions, in Karelia and in the southern region of Lake Baikal. Fire dynamics were more complex than in the Republic of Komi, as they did not follow the same trend of gradual decline in the FRI.

Mots-clés : Feu, forêt boréale, Holocène, Russie, reconstruction des températures issues des grains de pollen, GDGs, REVEALS

Keywords: Fire, boreal forest, Holocene, Russia, pollen-inferred temperatures, GDGs, REVEALS