From vegetation zones to climatypes: effects of climate warming on Siberian ecosystems

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INTRODUCTION

Evidence for global warming over the past 200 years is overwhelming (Hulme et al. 1999), based on both direct weather observation and indirect physical and biological indicators such as retreating glaciers and snow/ice cover, increasing sea level, and longer growing seasons (IPCC 2001). Recent GCM projections of the Hadley Centre (Gordon *et al.* 2000) for Siberia show an increase in temperature of 4 ^{o}C to 6 ^{o}C and an increase in precipitation of as much as 25% by 2100. These changes, moreover, could occur at a rate of 0.1^{o}C to 0.4^{o}C per decade (Watson *et al*., 1996).The rapid rate of change coupled with the large absolute amount of change is expected to have profound effects on plants of the boreal forests at all hierarchial levels: from forest zones (Monserud *et al*., 1993), to ecosystems (Guisan *et al*. 1996), to species (Iverson and Prasad 1998, Box *et al.* 1999), to populations within species (Rehfeldt *et al.* 1999b, 2002).

Our goals are to estimate effects of a warming climate on Siberian vegetation, first, at the highest level of organization, and, second, the lowest. The first considers the effects of global warming as zonal vegetation shifts across the plains and plateaus of central Siberia, and the second considers intraspecific effects within the mountains of southern Siberia. For the second objective, we invoke Turesson's concept of climatypes, the climatic ecotypes that comprise species, and illustrate intraspecific effects for *Pinus sylvestris* and *Larix sibirica*.

METHODS

Study area.

Our studies of the effects of global warming on vegetation zones deal with the plains and tablelands of central Siberia, roughly 90-120^{o}E longitude and 50-75^{o}N latitude. Studies of the effects of global warming on climatypes deal with the southern mountains, the Sayan Mountains**,** bounded by 89-96^{o}E longitude and 50-56^{o}N latitude. Our base map for this region was a 1 km grid (GLOBE, 2000) which contained 5,600,000 pixels for the plains and tablelands and 420,000 pixels for the southern mountains.

Mapping current climates.

January and July temperatures, growing degree-days, base 5 °C (GDD_5); negative degree-days, base 0°C (NDD_0); and an annual moisture index (AMI), the ratio of GDD_5 to mean annual precipitation were proven to be useful in previous analyses addressing plant responses to climate (Tchebakova et al., 1994; Rehfeldt *et al.* 1999a, 2002). We assembled these data normalized for the period 1900-1964 from 200 weather stations across Siberia, 60 of which were in the Sayan Mountains (Reference books, 1967-1970). We used Hutchinson's (2000) thin plate splines to produce climatic surfaces of these variables on our base map using the 1 km grid. Climatic and topographic images were visualized using IDRISI32 (Eastman, 2000). The AMI surface was calculated by dividing the GDD_5 image by the annual precipitation image.

Mapping future climates.

For predictions of global warming, we used the greenhouse gas scenario from the Hadley Centre, HadCM3GGa1 (Gordon *et al.* 2000) for the decade beginning in 2090. This scenario estimates winter temperature increases of 3 to 9^{o}C, summer temperature increases of 4 to 6^{o}C, and annual precipitation changes (in percentage) between –4 and +25% over the study area (Fig. 1). Future January and July temperatures and annual precipitation for each pixel were calculated from the change in monthly means for temperature and annual average for precipitation between the normalized period and the future decade (Fig. 1). Future values of GDD_5 and NDD_0 were calculated using the following linear regressions: GDD_5 was calculated from mean July temperature (R^2= 0.90), NDD_0 from January temperature (R^2=0.96). Future values of AMI were directly calculated dividing the future GDD_5 image by the future annual precipitation image.

Vegetation zones.

The Siberian bioclimatic model of Tchebakova *et al*. (1994) was modified to predict vegetation zones (types) from three bioclimatic parameters: GDD_5, NDD_0, and AMI. From the physiologic viewpoint, GDD_5 represents plants' requirements for warmth; NDD_0 characterizes plants' cold tolerance, and AMI representing a ratio of GDD_5 to annual precipitation characterizes plants' drought tolerance (Rehfeldt et al., 2002).

Seven major vegetation types are recognized by geobotanists on the plains of central Siberia: 1. Tundra; 2. Forest-tundra and sparce forest; 3. Dark-needled (*Pinus sibirica, Picea obovata,* and *Abies sibirica*) taiga (northern, middle, southern) on elevated tablelands; 4. Light-needled (*Larix sibirica* and *Larix gmelinii, Pinus sylvestris*) taiga (northern, middle, southern); 5. Birch (*Betula pendula* and *Betula pubescens*) and light-needled (*Larix sibirica* and *Pinus sylvestris*) subtaiga; 6. Birch (*Betula pendula* and *Betula pubescens*) and light-needled (*Larix sibirica* and *Pinus sylvestris*) forest-steppe; 7. Steppe (Shumilova, 1962; Isachenko, 1988).

In our bioclimatic model, the annual moisture index separates vegetation into two large types**,** arboreal and non-arboreal (forests and steppes), and further subdivides the former type into dark-needled and light-needled forests. The cold parameter, NDD_0, also tends to separate dark-needled and light-needled tree species. In Siberia, permafrost prevents dark-neelded species from spreading eastward across Asia (Shumilova. 1962), although summers are sufficiently warm to allow to survive as far east as Yakutia. The dark- and light-needled forest zones are further separated into latitudinal subzones (e.g. forest-tundra and sparse forests, northern, middle and southern taiga, forest-steppes) by GDD_5. Because southern taiga and subtaiga are not separated by GDD_5 these two types were combined into one zone. Although steppe, semidesert-desert, broadleaf forest and temperate forest-steppe types are not found under current Siberian climate, these four classes are included into our model because of their potential importance under a warming climate. In total, therefore, our model considers 13 vegetation types, each of which can be defined climatically (Table 1).

Climatypes

The distributions of *P. sylvestris* and *L. sibirica* were subdivided into climatypes using the results of Rehfeldt *et al.* (in press). These results were based on common garden studies that had been established across the former Soviet States. In such studies, seeds from numerous native populations are moved to and grown on an array of climatically disparate test sites. Because seeds are transferred along climatic gradients, such studies can also be viewed as climate-change experiments. Differential performance of populations then reflects adaptive differences among populations that have accrued from natural selection in the climate of the provenance where the seeds originated. The results of such studies can be used to define a climatype as the climatic limits for a group of populations whose individuals are adapted to same or similar climate.

The analyses of Rehfeldt *et al*. (in press) used published data on the height and survival of 313 populations of *P. sylvestris* that had been planted on 36 sites and of 130 populations of larch (63 of *L. sibirica*, 42 of *L. gmelinii*, and 25 of *L. sukaczewii*) planted on 8 sites. These data were used to develop transfer functions that predicted 12-year height from the difference in climate between the provenance of a population and the planting site. The functions were based on a Weibull model which is Gaussian but can be asymmetric. For both height and survival, five transfer functions were developed, those driven by GDD_5, NDD_0, and AMI are used herein.

The transfer functions showed that height and survival decrease as transfer distanced either increased or decreased from an optimum value which tended to be close to zero, the climate of the provenance. Confidence intervals about the vertex of the function were used to estimate (see Rehfeldt, Tchebakova and Barnhardt, 1999a**)** the climatic distance separating genetically different populations. For *P. sylvestris*, the limits were ±240 GDD_5, ±575 NDD_0, and ±0.6 units of AMI, and for *L. sibirica* as ±325 GDD_5, ±1150 NDD_0, and ±0.5 units of AMI. Because these limits reflect the distance that seeds can be moved from their provenance before growth and survival begin declining, they also reflect the climatic breadth of a climatype.

Climatypes were defined by subdividing the climatic distribution of the species into classes bounded by these limits. Because the 313 pine provenances used in these tests ranged from 626 to 2916 GDD_5, 5 classes, 480 degree-days in breadth, were required to encompass the species distribution. Six classes were needed for both NDD_0 and AMI. All possible combinations of these classes produced an upper limit to the number of pine climatypes at 180. For the larch, there were 8 classes for the moisture index, 3 for GDD_5, and 2 for NDD_0 which produced a maximum of 48 climatypes.

Climatypes defined in this manner must be considered as potential climatypes because many may not exist (*e. g.*, high GDD_5 coupled with low NDD_0). Other combinations may exist, but on the landscape may be occupied by species that have competitively excluded either *P. sylvestris* of *L. sibirica.* In the Sayan Mountains, for instance, the pine and larch rarely occur in climates inhabited by the dark-needled conifers even though they are capable of growing there (Ermolenko, 2001). Nonetheless, for our analyses of intraspecific effects of a changing climate, we will assume that all climatypes exist.

Climatypes of both species were mapped for the Sayan Mountains using the climate maps of GDD_5, NDD_0, and AMI produced above. Mapping was done for the contemporary climate and for the climate expected by the Hadley GCM for the decade beginning in 2090.

RESULTS

Vegetation zones.

Estimates of the area occupied by zonal vegetation types in current and future climates of central Siberia are given in Table 2.

In the contemporary climate East of Yenisei River, light-needled taiga prevails, with *Larix sibirica* and *L. gmelinii* being the domimant species. *Pinus sylvestris* can also dominate these forests in the warmer climates of the south or on sandy soils wherever they may occur. Dark-needled species appear in moist and warm climates, such as those along of the Yenisei Ridge at the mid-latitudes (60^o E), in the Sayan Mountains in the south, and in the West Siberian Plain which is west of Yenisei River and south of 64^{o}N. At the high latitudes of Putoran Mountains (north of the the Artic Circle), only larch taiga can withstand the cold climate and permafrost, although *Picea obovata* and *Pinus sibirica* may be mixed with *Larix* in the large river valleys which tend to be warmer than the surrounding landscape. In the current climate, northern vegetation types like tundra, forest-tundra, and northern taiga cover about 60% of the landscape. About a quarter of the territory is under middle taiga, most of which is light-needled. Only 10% of the region is occupied by a southern taiga, in which dark and light taiga and subtaiga are equally represented. No grasslands are shown by our model north of 56^{o}N (Fig. 2a).

Enormous changes in the vegetation cover of central Siberia are projected for a warmed climate (Table 2; Fig. 2b). Southern vegetation types such as southern taiga, subtaiga, and forest-steppe are expected to expand from about 10% to 70% coverage. This increase in coverage would be largely at the expense of northern and middle taiga each of which would then occupy less than 20%. Forest-tundra and sparse forests would nearly dissappear, while tundra and bare lands should disappear completely. These latter types would be replaced primarily by forest-tundra and dark-needled taiga in the Putaran Plateau and by dark-needled taiga in the Anabar Plateau. In a warmed climate, the forest-tundra which currently surrounds both of the northern plateaus should be replaced by light-needled taiga and even forest-steppe. Forest-steppe also is expected to reach the Putoran Plateau which is more than 1000 km north of the contemporary distribution of this vegetation type.

Although forest-steppe, steppe, and semidesert do not exist in current climate of central Siberia, these vegetation types are expected to occupy 50% of the study area in the climate of 2090. Large areas of steppe are projected for the central Yakutian Plain and the Tungus Plateau, while semi-desert should cover a significant area on the Angar Plain.

Our model also shows that two additional vegetation types that currently do not exist in Siberia should occur there in a warmed climate. One is the temperate forest-steppe, found by analogy from our global vegetation model (Tchebakova *et al*., 1993). This type should cover a large area on the plains and tablelands where mainly dark-needled taiga occur today (between latitudes 56^{o}N and 60^{o}N and longitudes 90^{o}E and 100^{o}E). The second novel type is the temperate broad-leaved forest which is expected to appear in the small valley of Velmo River (about 93^{o}E and 63^{o}N). Because the climate-change scenario we are using predicts a high degree of warming for Siberia, the concomitant invasion of broadleaved species into central Siberia seems reasonable. This is supported further by Khotinsky (1977) who reconstructed past vegetation from pollen depositions and concluded that birch and other broad-leaved forests once were distributed east of the Ural Mountains as far as 70^{o}E and 57^{o}N into the West Siberian Plain.

Climatypes

P. sylvestris. Of the 180 possible climatypes (Table 3), 26 were found for the contemporary climate in the Sayan Mountains (Fig. 3 a and b). These 26 occupy 71 % of the region, leaving 29 % (class #0) beyond the climatic limits of distribution of the pine for at least one of our three climate variables. Note, however, that these results do not imply that pine occurs across 71 % of the region; in fact, cover types show that the pine in reality occupies only about 10 %, with much of the region inhabited by dark-needled species which competitively exclude the pine. Of the 26 climatypes of today, most are minor (Table 3); twelve, in fact, account for less than 0.5 % of the total area (<1575 sq. km). Only five climatypes cover more than 5 % (15,750 sq. km), and of these, #4 and #46, are mammoth, accounting for 16 and 20 % of the total area (Table 4).

Figure 3 b shows the distribution of climatypes expected in the Sayan Mountains for the projected climate of 2090 according to the Hadley GCM. This figure suggests that the future climate should become more amenable for the pine, with *P. sylvestris* climatypes then encompassing all but 9 % of the region (Table 4, Fig. 3 b). The increase amounts to 20 % of the total land area (about 63,000 sq. km) climatically suitable for the pine. Likewise, the number of climatypes suitable for the region should increase from 26 to 35 (Table 4), but again, many (18) of these should account for < 1 % of the area. Of the 35, three (#40, #82, and #88) are, accounting for 12 to 15 % of the total area.

A comparison of the current and future distribution of climatypes (Fig. 3) shows that by the end of this century, there should be a complete redistribution of climatypes across the entire region. Two of the three most important climatypes of the future, #82 and #88, do not exist in the region today (Table 3). The third, #40, which is expected to cover 12% of the region in the future, currently occupies only 4.6 %. The two huge contemporary climatypes, #4 and #46, should still be present in the future but are expected to occupy only about 5 % of the total area. Twelve climatypes that occur in the region today are not expected to be present in the future, and 23 that should be present in the future do not occur in the region today. Even though contemporary and future climates are expected to have only 13 climatypes in common, their geographic locations should change greatly. Indeed, except for their physiognomic basis, Figures 3 a and b have very little in common.

Larix sibirica. Of the 48 possible combinations of our climate classes (Table 5), 24 occur today within the Sayan Mountains (Table 6, Fig. 4 a). These climatypes cover approximately 67 % or the region, thus suggesting that 33 % lie outside the climatic limits of *L. sibirica*. Of the 24 climatypes, 11 cover < 1 % or the area and only 5 cover more than 5 %. Two of the climatypes, #1 and #3, are huge, covering 19 % and 17 % of the total area, respectively. These two, therefore, account for almost one-half of the area that is climatically suitable for larch (Fig. 3 a).

The climate in the decade beginning in 2090 is expected to become more amenable to larch, with about 92 % of the land then lying within the species climatic limits (Fig. 4 b, Table 6). This represents an increase of 24 %, or about 75,500 sq km. This greater suitability for larch in the future climate is also reflected by the presence of 34 climatypes, an increase of 10. As a result, 71 % of all of the potential larch climatypes should be found within the Sayan Mountains. As before, however, only six of the climatypes should occupy more than 5 % of the region, and of these, only one, #20, is huge.

Figure 4 a and b, illustrates the change in the distribution of climatypes that would be expected for the decade beginning in 2090. While the present and future climates should have 20 climatypes in common, their relative importance (Table 6) and geographic positions (Figs. 3 B) change greatly. Climatypes #1 and #3, which are huge in the contemporary climate, should occupy < 5 % of the area in the future. Likewise, climatype #20, which should dominate in the future climate, covers <1 % of the area today. In total, 7 climatypes that occur in the region today are not expected in the future, and 14 that should be present in the future do not occur in the region today. As for *P. sylvestris*, the changing climate will have far reaching effects on the distribution of *L. sibirica* climatypes in the Sayan Mountains.

DISCUSSION

Climate-change obviously will alter the adaptedness of forest tree species that are composed of climatypes. Genotypes of sessile forest trees simply can not track their optimal climate as it changes. Our results join with those on *Pinus contorta* (Rehfeldt *et al.*, 1999b, 2001) and *P. sylvestris* (Rehfeldt *et al.* 2002) to illustrate that intraspecific adjustment to change will not be trivial. Adjusting to global warming will require a wholesale redistribution of genotypes across the landscape to realign climatypes in the novel climates and thereby maintain optimal forest growth and productivity (Rehfeldt *et al.* 2001). Response to climate-change, therefore, is much more than a shifting of species distributions (Davis and Shaw 2001). Indeed, effects of a changing climate reverberate throughout a species'distribution as genotypes become reshuffled across the landscape (Rehfeldt *et al.*, 1999b, 2002).

Our analyses suggest that by 2090, the climate of the Sayan Mountains should be more amenable for both *P. sylvestris* and *L. sibirica* than it is today. Nonetheless, the distribution of climatypes is expected to undergo a complete overhaul. The prominent climatypes of today should either be absent from or minor in the future forests. Likewise, the most prominent climatypes expected in the future are either absent or minor today. Even those climatypes that should remain in the landscape throughout the present century are expected to change in position and importance. To be sure, climate-change as predicted by the Hadley GCM should have widespread effects on the distribution of genotypes within these species.

As an indication of the scope of these intraspecific effects, it is instructive to assess the contemporary location of the climatypes expected to be of future importance in the Sayan Mountains. Of the three *P. sylvestris* climatypes expected to dominate future forests, one, #40, is a minor component of the contemporary array. Nevertheless, this climatype is much more prevalent today toward the southwest in the foothills of the Altai Mountains, nearly 700 km away. Climatypes #82 and #88, which will be new to the Sayan Mountains, are currently present as isolated populations in Kazakhstan and Bashkiria, about 1500 km and 20 degrees of longitude to the west. And, for *L. sibirica,* climatype #20, which is to be of future importance, also is present today in the Altai Republic. However, the climatic conditions with which this climatype is associated also can be found west of the Ural Mountains in European Russia. Because the dominant larch west of the Ural Mountains is *L. sukaczewii,* it is possible that the future climates of the Sayan Mountains may be suited to a mixture of larch species and their hybrids. Regardless, it is clear that the genotypes expected to be of importance to the future vegetation of the Sayan Mountains currently reside at long distances from their future habitat. These distances further illustrate the magnitude and complexity of the intraspecific adjustments necessary for the forest vegetation of the future to become physiologically attuned to the novel climate.

Migration and natural selection undoubtedly are the processes that will control the evolutionary adjustments necessary for plants to accommodate a changing climate. While migration is the only feasible means by which genotypes can invade and become established in climates beyond their contemporary distributions, natural selection is the process by which genotypes change when exposed to novel climates. Although rates of migration tend to be slow (Davis 1989), responses to selection can be rapid. Nonetheless, there is a limit to the amount that genetic systems can change in a single generation of selection. Estimates for *P. contorta* (Rehfeldt *et al.* 2001) and *P. sylvestris* (Rehfeldt *et al.* 2002) suggest that for Siberia, 5 to 10 generations may be required for the evolutionary process to adjust to global warming. This process, therefore, may take several centuries even where species' distributions are not changing.

Migration becomes even more problematic when dealing with the vegetation shifts illustrated in Fig. 2. Obviously, vegetation zones of either the plains or mountains will not shift as a unit. Individuals migrate, and, as a result, contemporary plant associations may or may not re-assemble in the novel climates. Nonetheless, the paleogeographic record demonstrates that the process by which migrants adjust to novel climates is complex and slow, requiring millenia. Because ongoing climate warming (3-6^{o}C) is predicted to occur for 50-100 years, changes in vegetation due to migration should, first, lag far behind the climatic shifts (see Tchebakova et al,

1994) and, second, disrupt vegetation zones. Only seven species can withstand the severe contemporary climates of Siberia: five conifers (*Pinus sibirica, Picea obovata, P. sylvestris, Larix* spp., and *Abies sibirica*) and two broadleafs (*Betula pendula* and *B. pubecens* and *Populus tremulus*). Until natural selection adjusts the available genetic variability, it is concievable that none of the available genotypes of these species would be suited to the novel climate. If a species occurs under conditions beyond its climatic optimum it declines. For example, the southern tree border of species distributions are expected to shift northwards because of moisture stresses will increase. A favorable climate, moreover, would promote competetive abilities of species inhabiting their climatic optima, and these species may become dominating. For example, the growth of dark-needled species like *Pinus sibirica* and *Abies sibirica* is expected to be enhanced in the middle taiga in a warmed climate. So, vegetation redistribution would depend on the joint actions of seed dispersal and environmental selection, with the latter determining which genotypes of which species become, first, established and, second, competitively exclusive. However, in the mountains vegetation redistribution due to tree migration seems feasible over short periods of 50-100 years. This is because migration of adapted genotypes across mountainous landscapes only needs to occur across a few hundred meters in order for genotypes to track the climate to which they are adapted optimally. For this reason, mountains readily serve as refuges during times of extripation.

Fire is another factor that is capable of influencing the speed by which vegetation adjusts to climate-change. In the short term, fire will aid the redistribution of vegetation by opening for colonization sites previously occupied. In fact, forest fire successions are predicted to dominate central Siberia (Furyaev et al., 2001), and in doing so should increase the abundance of *Betula* spp. in warm zones and *Larix* spp. in cold zones.

In accounting for the effects of climate-change on the vegetation, permafrost cannot be ignored. To be sure, permafrost is the principal factor controlling the distribution of vegetation in central Siberia and Yakutia. First, it allows forests to develop in areas where otherwise semideserts would occur (Shumilova, 1962). Second, it limits the eastward spread of dark-needled species (*Pinus sibirica*, *Picea obovata* and *Abies sibirica*) in the Siberia. Inside the permafrost zone, these dark-needled species can reach high latitudes only in sandy soils along river valleys and benches where permafrost may thaw as deep as 1-1.5 m (Shumilova, 1962). *Larix gmelini* and *L. cajanderi*, by contrast, may grow on soils which thaw only about 10-30 cm in summer (Abaimov et al., 1999). Under the climate-change scenario we used in this study, the heat resources will be available for melting permafrost. From Stefan's formula (Dostavalov, Kudriavtsev, 1967), we estimated the ratio of the depth of the freezing layer during contemporary winters and those expected under a changing climate (Fig. 4 a) and the ratio of the depth of the thawing layer during contemporary summers and those expected under a changing climate (Fig. 4b). The depth of the freezing (or thawing) layer is proportional to the square root of the ratio NDD_0 (or GDD_5) in future to current climates. At the highest latitudes, much milder winters and warmer summers should promote a rapid demise of the permafrost, especially in mountains. As a result, dark-needled species would be expected to track the retreating permafrost and thereby invade the Taymyr Peninsula and the Putoran and Anabar Plateaus, which are currently dominated by tundra and forest-tundra. The presence of dark-needled species at these locations during warm epocs is supported by pollen spectra (Khotinsky, 1977) from the mid-Holocene. In the middle latitudes covering about 65% of our area, the depth of thawing should increase by 40-60%. This amount of thawing most likely is not sufficient for allowing dark-needled species to become established. As a result, light-needled taiga would dominate this area. In the south, the thawing layer is predicted to increase only 20-40%, an amount that should allow forest-steppes and steppes to develop.

A tremendous amount of water stored in the permafrost of the northern plains and mountains is expected to be released under rapid warming. The release of this water undoubtedly will have a large impact on the Siberian landscapes. A part of this water collected from the basins of two big rivers Lena and Khatanga will flow directly into the Arctic ocean and may flood the coastal area between Khatanga and Olenek bays. Another part of the water collected from the basins of other two big rivers Nizhniaia Tunguska and Kureika will flow into the Yenisei River near the North Circle. Our rough estimates of the possible flooding of its lower left bank occurring in the West Siberian Plain show that it may cover at least 1-2 kilometers.

All together, our analyses thus demonstrate the far-reaching effects of a changing climate on the ecologic distribution and genetic composition of future forests. Forest zones and species boundaries are expected to change at the same time that genotypes within species will be redistributed within species. Because analogs to the future forests of Siberia exist within the present-day distributions, there is no doubt that the vegetation is capable of adjusting to the predicted changes. Current estimates, however, suggest that redistribution of forest zones and climatypes will require long periods to adjust to the amount of change being predicted. From the ecological perspective, therefore, it is the speed of warming rather than the absolute amount of warming that is most foreboding. Indeed, the lag in vegetal response to rapid change suggests that if the climate does not stabilize, the vegetation may never be able to approach equilibrium. From the practical viewpoint, therefore, it seems obvious that maintaining optimal levels of productivity to for Siberian forests will require the participation of mankind in the natural processes to assure that the appropriate species and genotypes appear in the appropriate climates in a timely manner.

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Table 1 Climatic limits for the modified Siberian model of Tchebakova et al. (1994).

Vegetation type	GDD_5		AMI		NDDo	
	Lower limit	Upper limit	Lower limit	Upper limit	Lower limit	Upper limit
Tundra	None	<300	None	None	None	None
Forest-tundra and sparse taiga	300	500	None	None	None	None
Northern dark-needled taiga	500	800	None	<1.5	>-4500	None
Northern light-needled taiga	500	800	>1.5	None	None	<-4500
Middle dark-needled taiga	800	1050	None	<1.5	>-3500	None
Middle light-needled taiga	800	1050	>1.5	None	None	<-3500
Southern dark-needled taiga and birch subtaiga	1050	1250	None	<2.25	None	None
Southern light-needled taiga and subtaiga	1050	1250	>2.25	None	None	None
Forest-steppe	1250	1650	None	<3.25	None	None
Steppe	1250	1650	>3.25	None	None	None
Semidesert/Desert	>1650	None	None	None	None	None
Broadleaf forest	1250	1650	None	<1.5	None	None
Temperate forest-steppe	>1650	None	1.5	3.25	None	None

Table 2. Areas (10^4 km^2) of vegetation zones in Siberia in current and warmed climates

Vegetation zone	Current climate	Proportion, %	Warmed climate	Proportion, %
Bare land	3.6	1.3	-	-
Tundra	35.8	12.5	0.1	0.0
Forest-tundra and sparse taiga	54.3	19.0	1.6	0.6
Northern dark-needled taiga	22.5	7.9	17.8	6.2
Northern light-needled taiga	62.5	21.9	3.2	1.1
Middle dark-needled taiga	3.1	1.1	12.6	4.4
Middle light-needled taiga	75.3	26.4	17.0	6.0
Southern dark-needled taiga and birch subtaiga	13.1	4.6	9.2	3.2
Southern light-needled taiga and subtaiga	15.2	5.3	56.1	19.6
Forest-steppe	0.3	0.1	99.0	34.7
Steppe	-	-	22.6	7.9
Semidesert/Desert	-	-	19.4	6.8
Temperate Broad-leaf forest	-	-	0.6	0.2
Temperate Forest-steppe	-	-	26.5	9.3
TOTAL	285.7	100	285.7	100

Table 3. 180 possible combinations of climatic indices (GDD_5, AMI and NDD_o) for pine climatypes in Russia

Annual moisture Index/ Growing Degree-days, 5°C	Negative Degree-Days, 0°C					
	-6000--4850	-4850--3700	-3700--2550	-2550--1400	-1400--250	-250-0
0.6-1.8/ 600-1080	1	2	3	4	5	6
1.8-3.0/ 600-1080	7	8	9	10	11	12
3.0-4.2/ 600-1080	13	14	15	16	17	18
4.2-5.4/ 600-1080	19	20	21	22	23	24
5.4-6.6/ 600-1080	25	26	27	28	29	30
6.6-7.0/1080-1560	31	32	33	34	35	36
0.6-1.8/1080-1560	37	38	39	40	41	42
1.8-3.0/1080-1560	43	44	45	46	47	48
3.0-4.2/1080-1560	49	50	51	52	53	54
4.2-5.4/1080-1560	55	56	57	58	59	60
5.4-6.6/1080-1560	61	62	63	64	65	66
6.6-7.0/1080-1560	67	68	69	70	71	72
0.6-1.8/1560-2040	73	74	75	76	77	78
1.8-3.0/1560-2040	79	80	81	82	83	84
3.0-4.2/1560-2040	85	86	87	88	89	90
4.2-5.4/1560-2040	91	92	93	94	95	96
5.4-6.6/1560-2040	97	98	99	100	101	102
6.6-7.0/1560-2040	103	104	105	106	107	108
0.6-1.8/2040-2520	109	110	111	112	113	114
1.8-3.0/2040-2520	115	116	117	118	119	120
3.0-4.2/2040-2520	121	122	123	124	125	126
4.2-5.4/2040-2520	127	128	129	130	131	132
5.4-6.6/2040-2520	133	134	135	136	137	138
6.6-7.0/2040-2520	139	140	141	142	143	144
0.6-1.8/2520-3000	145	146	147	148	149	150
1.8-3.0/2520-3000	151	152	153	154	155	156
3.0-4.2/2520-3000	157	158	159	160	161	162
4.2-5.4/2520-3000	163	164	165	166	167	168
5.4-6.6/2520-3000	169	170	171	172	173	174
6.6-7.0/2520-3000	175	176	177	178	179	180

Table 4. Areas (km^2) of seed zones for *Pinus sylvestris* in current and warmed climates in the Sayan Mts

Climatype number	Current climate	Proportion, %	Warmed climate	Proportion, %
0	93383	29.16	29282	8.9
2	5565	1.72		
3	21556	6.79	8676	2.67
4	47974	1576	18293	5.77
5			0.7	0.00
8	6618	2.03		
9	7985	2.47	4331	1.31
10	6004	1.99	67	0.02
14	1743	0.53		
15	1652	0.51	64	0.02
20	525	0.16		
21	253	0.08		
26	309	0.09		
32	70	0.02		
39	113		6884	2.16
40	13993	4.6	37131	11.99
44	1715	0.53		
45	798	0.25	19729	6.11
46	59278	19.87	12181	
50	6250	1.93		
51	2406	0.74	8779	2.69
52	16900	5.55	46	0.01
56	4592	1.41		
57	2835	0.87	2060	0.63
58	1625	0.53		
62	4020	1.22		
63	2143	0.66	617	0.19
68	1112	0.34		
69	495	0.15	86	0.03
76			9033	2.94
81			1201	0.38
82			44558	14.7
87			8522	2.64
88			43240	14.46
92			5	0.00
93			9929	3.06
94			12455	4.14
98			315	0.1
99			7367	2.27
100			3511	1.16
104			34	0.01

105			1610	0.49
106			72	0.02
118			35	0.01
124			8003	2.7
130			7914	2.62
134			24	0.01
135			453	0.14
136			4876	1.6
140			51	0.2
141			465	0.14
142			20	0.01

Table 5. 48 possible combinations of climatic indices (GDD_5, AMI and $NDD_{o)}$) for *Larix sibirica* climatypes in Russia

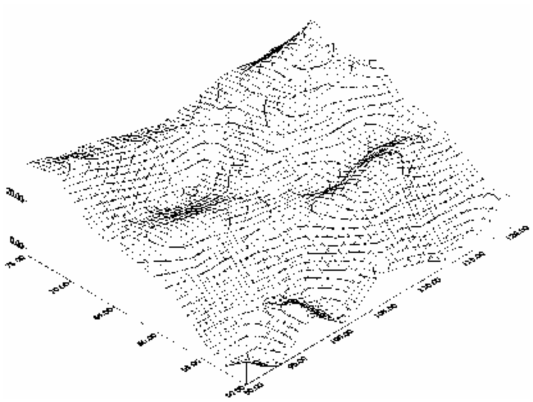
Annual moisture Index/ Growing Degree-days, 5°C	Negative Degree-Days, 0°C	
	–4500--2200	-2200--1200
0.8-1.8/ 650-1300	1	2
1.8-2.8/ 650-1300	3	4
2.8-3.8/ 650-1300	5	6
3.8-4.8/ 650-1300	7	8
4.8-5.8/ 650-1300	9	10
5.8-6.8/ 650-1300	11	12
6.8-7.8/ 650-1300	13	14
7.8-8.5/ 650-1300	15	16
0.8-1.8/ 1300-1950	17	18
1.8-2.8/ 1300-1950	19	20
2.8-3.8/ 1300-1950	21	22
3.8-4.8 / 1300-1950	23	24
4.8-5.8/ 1300-1950	25	26
5.8-6.8/ 1300-1950	27	28
6.8-7.8/ 1300-1950	29	30
7.8-8.5/ 1300-1950	31	32
0.8-1.8/ 1950-2350	33	34
1.8-2.8/ 1950-2350	35	36
2.8-3.8/ 1950-2350	37	38
3.8-4.8 / 1950-2350	39	40
4.8-5.8/ 1950-2350	41	42
5.8-6.8/ 1950-2350	43	44
6.8-7.8/ 1950-2350	45	46
7.8-8.5/ 1950-2350	47	48

Table 6. Areas (km^2) of seed zones for *Larix sibirica* in current and warmed climates in the Sayan Mts

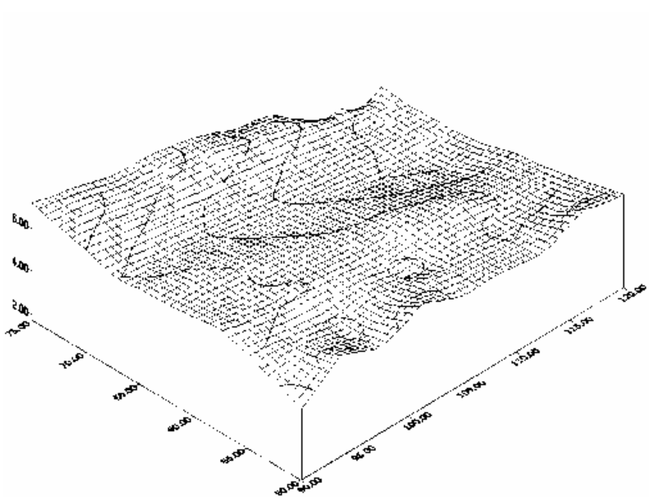
Climatype number	Current climate	Proportion, %	Warmed climate	Proportion, %
0	103636	32.53	26043	7.96
1	58330	18.84	26741	8.33
2	14945	4.95	19482	6.27
3	50777	16.68	12845	3.94
4	15064	5.03	142	0.04
5	20351	6.52	2325	0.7
6	2501	0.83		
7	6179	1.92	667	0.2
8	46	0.02		
9	2753	0.84	154	0.05
11	1355	0.41	3	0.00
13	552	0.17		
15	286	0.09		
17	261	0.08	5532	1.76
18	93	0.03	24060	7.85
19	4276	1.4	14863	4.65
20	2376	0.78	39466	12.97
21	4855	1.6	14191	4.4
22	4009	1.29	22296	7.41
23	5923	1.89	10619	3.27
24	1117	0.36	7489	2.48
25	3420	1.05	7789	2.39
26			1583	0.52
27	3755	1.15	4397	1.35
28			264	0.09
29	3264	0.99	2657	0.81
30			3	0.00
31	175	0.54	1167	0.36
36			3127	1.02
38			20078	6.76
39			0.8	0.00
40			23130	7.77
41			1020	0.31
42			8339	2.75
43			2207	0.68
44			4484	1.47
45			2700	0.83
46			4.4	0.00
47			2053	0.63

Fig. 1. Climate differences by 2090 according to the Hadley climate change scenario (2001)

A. Precipitation difference(%) between current and future climates in central Siberia



B. July temperature difference (^oC) between current and future climates in central Siberia



C. January temperature difference between current and future climates in central Siberia

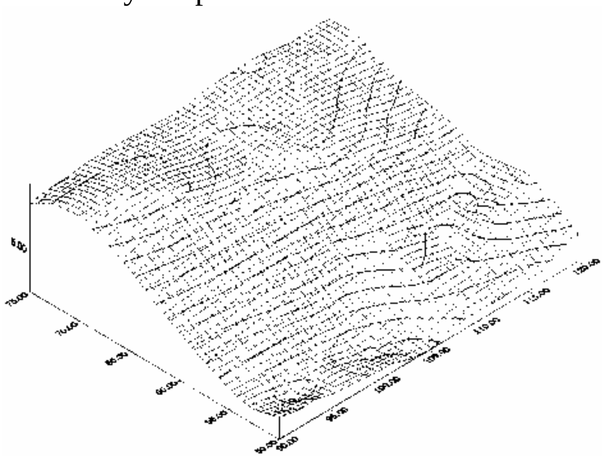


Fig. 2. Vegetation distribution in central Siberia in current (a) and a warmed (b) climates by 2090

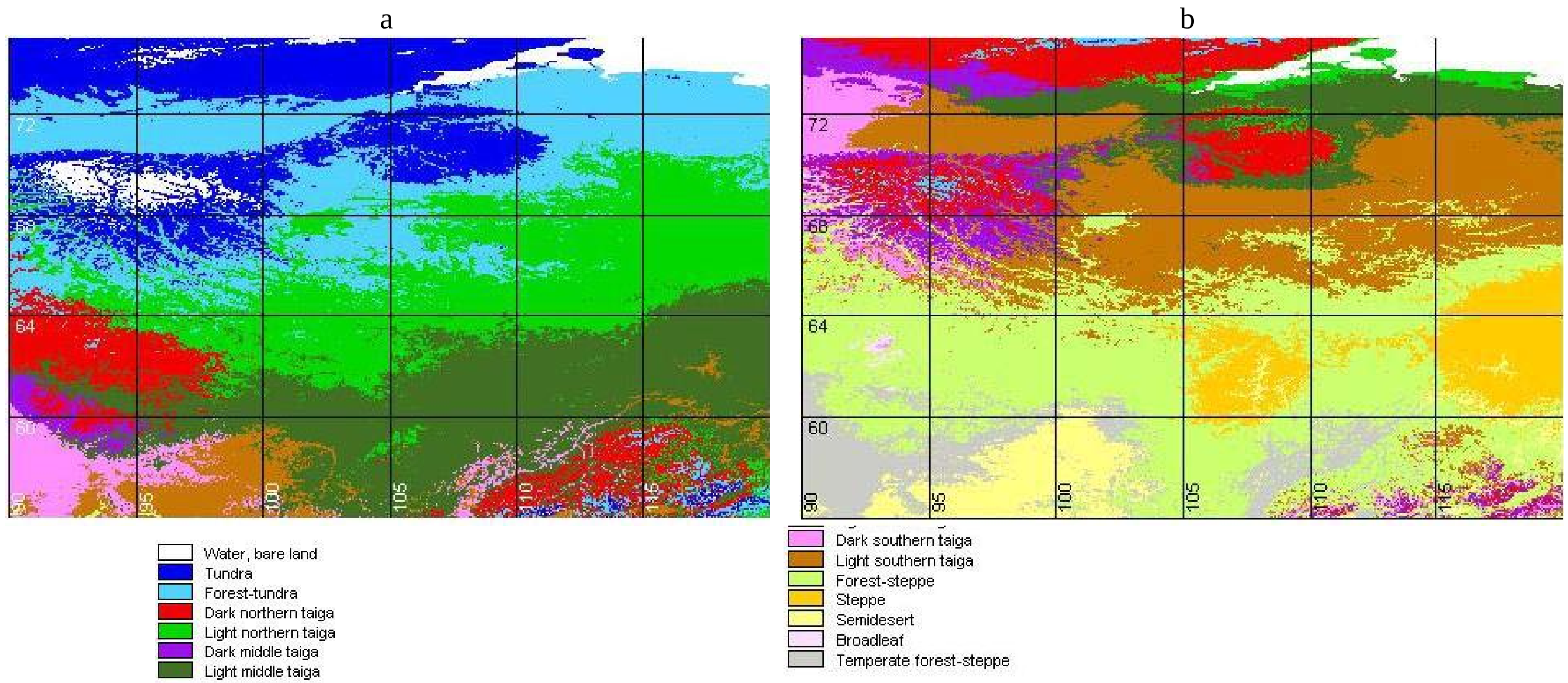


Fig. 3. Distribution of *Pinus sylvestris* climatypes in the Sayan mountains in current (a) and a warming (b) climates. Different colors are 180 climatypes according to Table 3. Not all climatypes are realized in actual climatic space. White means that pine does not occur in a given climate.

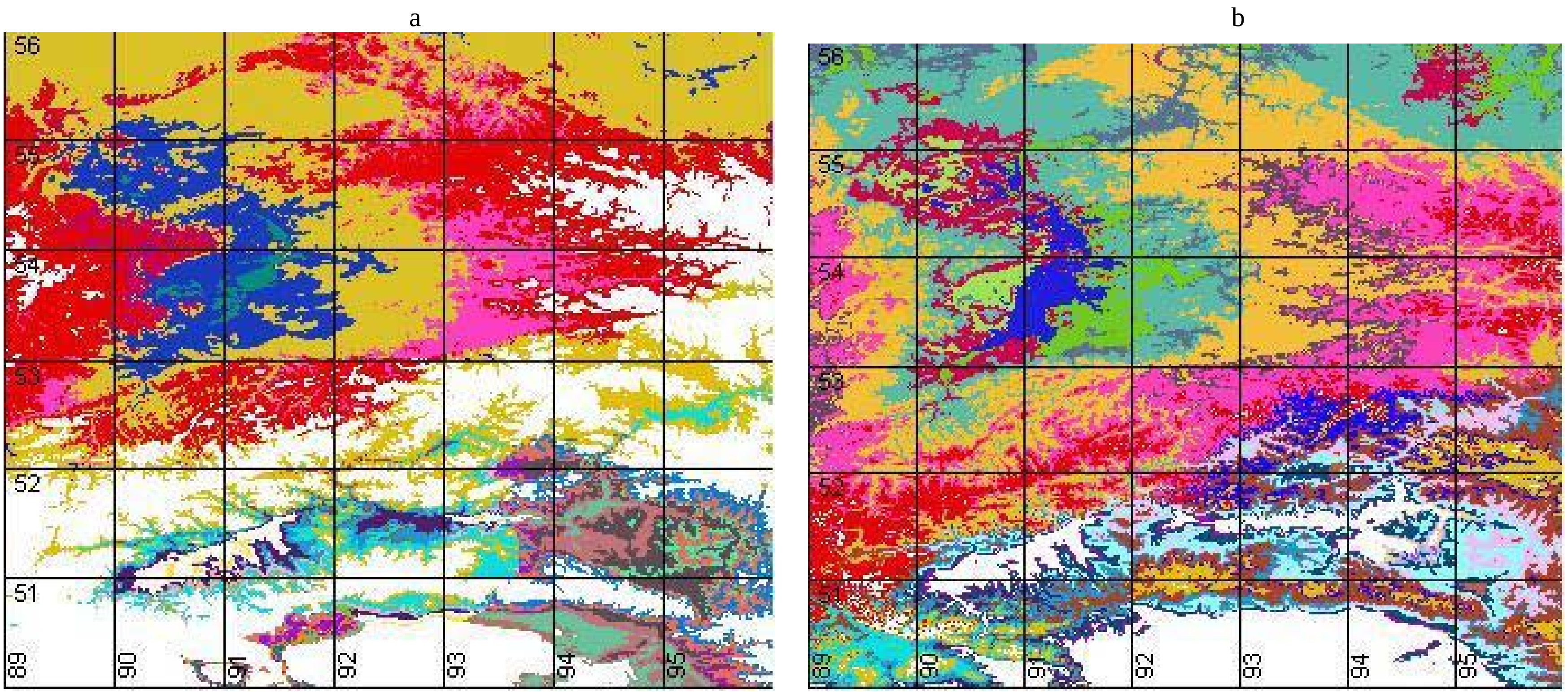


Fig. 4. Distribution of *Larix sibirica* climatypes in the Sayan mountains in current (a) and a warming (b) climates. Different colors are 48 climatypes according to Table 5. Not all climatypes are realized in actual climatic space. White means that larch does not occur in a given climate.

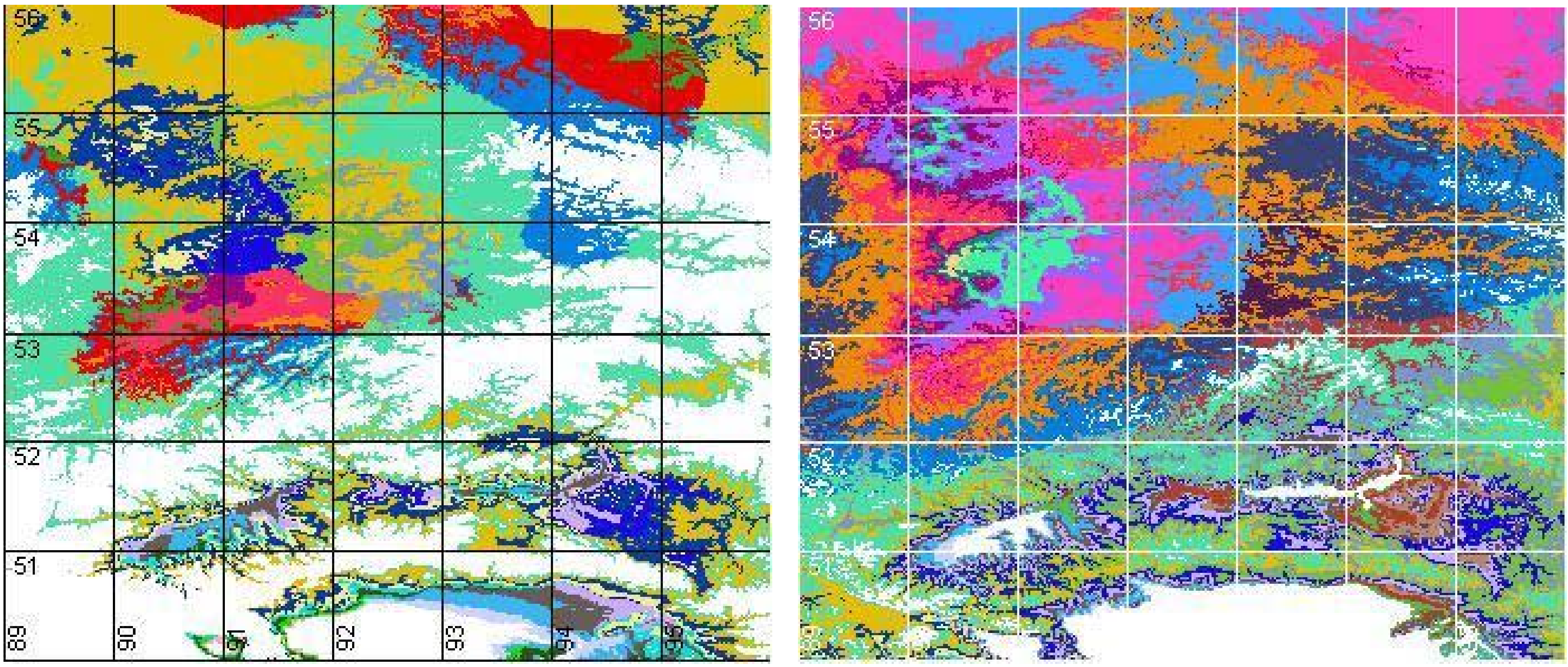


Fig. 5. Percentage of the freezing layer decrease (a) and thawing layer increase (b) by 2090 with respect to current climate