Springer Theses
Recognizing Outstanding Ph.D. Research

Qian Hao

The LGM Distribution of Dominant Tree Genera in Northern China's Forest-steppe Ecotone and Their Postglacial Migration

Springer

Springer Theses

Recognizing Outstanding Ph.D. Research

Aims and Scope

The series "Springer Theses" brings together a selection of the very best Ph.D. theses from around the world and across the physical sciences. Nominated and endorsed by two recognized specialists, each published volume has been selected for its scientific excellence and the high impact of its contents for the pertinent field of research. For greater accessibility to non-specialists, the published versions include an extended introduction, as well as a foreword by the student's supervisor explaining the special relevance of the work for the field. As a whole, the series will provide a valuable resource both for newcomers to the research fields described, and for other scientists seeking detailed background information on special questions. Finally, it provides an accredited documentation of the valuable contributions made by today's younger generation of scientists.

Theses are accepted into the series by invited nomination only and must fulfill all of the following criteria

- They must be written in good English.
- The topic should fall within the confines of Chemistry, Physics, Earth Sciences, Engineering and related interdisciplinary fields such as Materials, Nanoscience, Chemical Engineering, Complex Systems and Biophysics.
- The work reported in the thesis must represent a significant scientific advance.
- If the thesis includes previously published material, permission to reproduce this must be gained from the respective copyright holder.
- They must have been examined and passed during the 12 months prior to nomination.
- Each thesis should include a foreword by the supervisor outlining the significance of its content.
- The theses should have a clearly defined structure including an introduction accessible to scientists not expert in that particular field.

More information about this series at http://www.springer.com/series/8790

Qian Hao

The LGM Distribution of Dominant Tree Genera in Northern China's Forest-steppe Ecotone and Their Postglacial Migration

Doctoral Thesis accepted by Peking University, Beijing, China

Springer

Qian Hao
Institute of Surface-Earth System Science
Tianjin University
Tianjin, China

Supervisor
Hongyan Liu
College of Urban and Environmental Sciences
Peking University
Beijing, China

ISSN 2190-5053 ISSN 2190-5061 (electronic)
Springer Theses
ISBN 978-981-13-2882-4 ISBN 978-981-13-2883-1 (eBook)
https://doi.org/10.1007/978-981-13-2883-1

Library of Congress Control Number: 2018958510

© Springer Nature Singapore Pte Ltd. 2018
This work is subject to copyright. All rights are reserved by the Publisher, whether the whole or part of the material is concerned, specifically the rights of translation, reprinting, reuse of illustrations, recitation, broadcasting, reproduction on microfilms or in any other physical way, and transmission or information storage and retrieval, electronic adaptation, computer software, or by similar or dissimilar methodology now known or hereafter developed.
The use of general descriptive names, registered names, trademarks, service marks, etc. in this publication does not imply, even in the absence of a specific statement, that such names are exempt from the relevant protective laws and regulations and therefore free for general use.
The publisher, the authors and the editors are safe to assume that the advice and information in this book are believed to be true and accurate at the date of publication. Neither the publisher nor the authors or the editors give a warranty, express or implied, with respect to the material contained herein or for any errors or omissions that may have been made. The publisher remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

This Springer imprint is published by the registered company Springer Nature Singapore Pte Ltd.
The registered company address is: 152 Beach Road, #21-01/04 Gateway East, Singapore 189721, Singapore

Supervisor Foreword

Forests account for 30% of the global land area, and they have important regulatory roles in the water cycle and biogeochemical cycle of the entire earth. However, climate change has led to increasing forest mortality rates worldwide; thus, the forest dynamic is an important ecology issue under future climate change, which needs long-term study.

In her thesis study, Dr. Qian Hao selected the forest-steppe ecotone in China as the main study areas, where the vegetation is sensitive to climate change. She has combined different approaches of paleoecology, phylogeography, and ecological modeling to reconstruct the glacial refugia and postglacial migration of three dominate forest genera (*Pinus*, *Quercus*, and *Betula*) in northern China. Through the studies of different temporal and spatial scales, she got three main conclusions: (1) the postglacial migration was multidirectional, including not only the long-distance migration process from low to high latitudes but also the process of local diffusion from northern refugia; (2) except the latitudinal migration, the vertical migration altered the changes of forest-steppe border to the Holocene climate changes; (3) there were various responses of local forests to climate change, including decreasing forest coverage, shrub expansion, and replacement of steppe. In sum, the results and major findings of the study can help us to understand the forest migration patterns comprehensively and the factors influencing the forest dynamics. This study will be useful for the fields of forest ecology, paleoecology, and biogeography.

College of Urban and Environmental Sciences
Peking University, Beijing, China
August 2018

Hongyan Liu

Preface

Studying dynamics of forests that occupy 30% of the land surface area has been becoming a hotspot in ecology. Forest distribution change since the Last Glacial Maximum (LGM) is critical for validating models predicting future forest dynamics. On the regional and catchment scale, the different resilience of tree species and buffer effects from diversified land surface features lead to the complex forest distributions and migration patterns in the forest-steppe ecotone, which need to be investigated in a multidisciplinary approach.

The forest-steppe ecotone in northern China is located at the edge of East Asian monsoon influence, and the regional forest within the ecotone is sensitive to climate change. Based on high-resolution lacustrine sedimentary records, this study reconstructed the distribution changes of *Pinus*, *Quercus*, and *Betula* during and after the LGM. An interdisciplinary approach integrating methods of paleoecology, phylogeography, and ecological modeling was used to reconstruct their glacial refugia and postglacial migration in northern China. On the regional scale, eight high-resolution sediment records under similar climate conditions were selected to show altitudinal migration pattern of these three dominated tree genera and the role of topographical factors on the migration of the forest-steppe border. On the catchment scale, an 820 cm core in Huangqihai, located in the forest-steppe ecotone in northern China, was analyzed in order to specify the local forest dynamics reconstructed from pollen assemblage as response to the Holocene climatic change reconstructed from chemical element ratio in the sediment. The following conclusions are drawn from this study:

1) The postglacial dynamics of forest distribution included not only long-distance north-south migration but also local spread process from LGM refugia in northern China.

Our data supported the hypothesis of the mountainous refugia in northern China. Besides, the Otindag Sandy Land which serves as the northern limit of *Pinus tabulaeformis* distribution was for the first time proposed working as a local refugium. Hence, we suggest that the species was located further north than previously illustrated, albeit perhaps at very low density. We thus infer that postglacial migration of

P. tabulaeformis was multidirectional and implied local spread from various refugia as well as long-distance migration from central/southern China.

This study also used the fossil evidence and species distribution model to illustrate the distribution area of other three dominated tree species (*Quercus mongolica*, *Betula platyphylla*, and *Betula dahurica*) in northern China during the LGM. The results also showed that the mountains in northern China may be refugia, and the northern coastal region may also work as refugia, suggesting the existence of the local spread phenomenon for them.

2) The dynamics of forest included not only latitudinal migration but also altitudinal migration. Altitudinal migration altered the changes of forest-steppe border to the Holocene climate changes.

Tree species living in the forest-steppe ecotone were commonly controlled by climate, especially the monsoon evolution. However, forests not only migrated latitudinally between northern and southern regions but also showed changes in altitudinal distribution during the Holocene, which is mainly influenced by topographic factors. Areas with high altitude range can support more trees and altitudinal migration possibility. Altitudinal migration altered the changes of forest-steppe border to the Holocene climate changes, and different topographic conditions lead to the spatial heterogeneity.

3) The response modes of local forest to climate drying could be shrubland expansion and savannification other than the replacement of forest by steppe.

The Holocene climatic change of Huangqihai region captured in detail the regional-scale monsoon dynamics, especially the drying trend which was obvious during 4000 to 1000 cal year BP. The corresponding vegetation dynamics were characterized by a steppe-forest-steppe sequence. Besides replacement of forest by steppe, we found two alternative responses of vegetation to drought: shrubland expansion and savannification. The shrubland began to expand into the forest when the precipitation-brought Pacific monsoon weakened at about 4 cal ka BP. While the dry period persisted for thousands of years, we found a clear minimum in vegetation coverage during 2970 to 600 cal year BP.

Keywords Forest-steppe ecotone; LGM refugia; Vertical migration; Ecological response; Pollen; *Pinus tabulaeformis*; Holocene

Parts of this Thesis Have Been Published in the Following Journal Articles

- Hao, Q., de Lafontaine, G., Guo, D., Gu, H., Hu, F.S., Han, Y., Song, Z., Liu, H., 2018. The critical role of local refugia in postglacial colonization of Chinese pine: joint inferences from DNA analyses, pollen records, and species distribution modeling. Ecography 41, 592–606. Reprinted from (Hao et al., 2018). Copyright (2017), with permission from John Wiley and Sons
- Hao, Q., Liu, H., Liu, X., 2016. Pollen-detected altitudinal migration of forests during the Holocene in the mountainous forest–steppe ecotone in northern China. Palaeogeography, Palaeoclimatology, Palaeoecology 446, 70–77. Reprinted from (Hao et al. 2016). Copyright (2016), with permission from Elsevier
- Hao, Q., Liu, H., Yin, Y., Wang, H., Feng, M., 2014. Varied responses of forest at its distribution margin to Holocene monsoon development in northern China. Palaeogeography, Palaeoclimatology, Palaeoecology 409, 239–248. Reprinted from (Hao et al. 2014). Copyright (2014), with permission from Elsevier

Acknowledgments

First and foremost, I would like to thank Prof. Hongyan Liu, who supervised me for 5 years. I have benefited tremendously from his professional knowledge, earnest academic attitude, and modesty. What he has taught me is not only the research methods but also the character of integrity and responsibility. This thesis cannot be completed without his patient instruction, valuable suggestions, and warm encouragement.

Secondly, I thank Prof. Hongya Gu. She and her graduate Dongshu Guo gave me a lot of guidance during my experiments in her laboratory. With their help, the experiments were carried out smoothly. I also owe my appreciation to Prof. Feng Sheng Hu, who gave me the opportunity to study in his lab in UIUC. I would like to thank him and Dr. De Lafontaine Guillaume, who offered guidance in my data analysis, software application, and language correction.

Besides, I have benefited from many other teachers. Thanks to Prof. Youxu Jiang, Shilong Piao, Zehao Shen, Yiyin Li, and Zhiheng Wang, who gave me many comments and suggestions for my thesis. Thanks to Prof. Liping Zhou and Chengjun Ji for providing the laboratory and experimental conditions.

Finally, I thank all my colleagues in the laboratory for their assistance in coring the lake sediment, doing experiments, and revising this thesis. I am also grateful to all my classmates for their help during the 5 years.

This work was supported by the National Natural Science Foundation of China (grant numbers 41325002, 41530747, and 31321061), the National Key Research Development Program of China (2017YFA0605101), and the 111 Project (grant number B14001).

Contents

1 Introduction 1
1.1 The Impact of Climate Change on Forests 1
1.2 Importance of Forest-Steppe Ecotones to Climate Change Research 1
1.3 Advances in Research Methods of Forest Migration 2
1.3.1 Paleoecology 2
1.3.2 Phylogeography 3
1.3.3 Species Distribution Models 5
1.3.4 Comprehensive Integration of Various Research Methods 6
1.4 Advances in the Study of Glacial Refugia and Postglacial Forest Migrations in Northern China 6
1.4.1 Forest Refugia and Local Spread 6
1.4.2 Vertical Distribution and Vertical Migration of Forests 7
1.4.3 Various Responses of Local Forests to Climate Drought 8
1.4.4 Individual Responses of Species to Climate Change 8
1.5 Scientific Questions and Hypotheses 9
References 11

2 Research Area and Research Methods 17
2.1 Overview of the Research Area 17
2.1.1 Climate of the Research Area 17
2.1.2 Vegetation of the Research Area 17
2.2 Research Flow 19
2.3 Research Methods 19
2.3.1 Paleoecology 19
2.3.2 Establishment of a Regional Pollen Database 23
2.3.3 Phylogeography (Cytoplasmic DNA Analysis) 24
2.3.4 Present and LGM Species Distribution Modeling 25
References 26

3 Glacial Refugia and the Postglacial Migration of Dominant Tree Species in Northern China 31
3.1 Glacial Refugia and the Postglacial Migration of *Pinus tabulaeformis* 31
3.1.1 Distribution Change Based on Pollen Data Analysis 31
3.1.2 Genetic Diversity Within and Among *P. tabulaeformis* Populations 35
3.1.3 Simulated Present and LGM Distribution of *P. tabulaeformis* 43
3.1.4 Last Glacial Maximum Distribution and Postglacial Migration of *Pinus tabulaeformis* 45
3.2 Glacial Refugia and the Postglacial Migration of *Quercus mongolica* 49
3.2.1 Distribution Change Based on Pollen Data Analysis 49
3.2.2 Simulated Present and LGM Distribution of *Q. mongolica* 50
3.2.3 Last Glacial Maximum Distribution and Postglacial Migration of *Q. mongolica* 50
3.3 Glacial Refugia and the Postglacial Migration of *Betula platyphylla* and *Betula dahurica* 51
3.3.1 Distribution Changes Based on Pollen Data Analysis 51
3.3.2 Simulated Present and LGM Distribution of *B. platyphylla* and *B. dahurica* 51
3.3.3 Last Glacial Maximum Distribution and Postglacial Migration of *B. platyphylla* and *B. dahurica* 52
3.4 Chapter Summary 52
References 52

4 Effects of Vertical Migration on Local Vegetation 57
4.1 Study methods 57
4.1.1 Sediment Pollen Data Collection 57
4.1.2 Altitude Range Calculation 61
4.1.3 Soil Surface Pollen Records and Environmental Interpretation 62
4.2 Temporal and Spatial Change of Arboreal Pollen Percentages During the Holocene 63
4.2.1 Temporal and Spatial Change of *Pinus* 63
4.2.2 Temporal and Spatial Change of *Quercus* 65
4.2.3 Temporal and Spatial Change of *Betula* 65
4.2.4 Temporal and Spatial Change of Arboreal Pollen 66
4.3 Effect of Different Factors on Soil Surface Arboreal Pollen Percentages 66