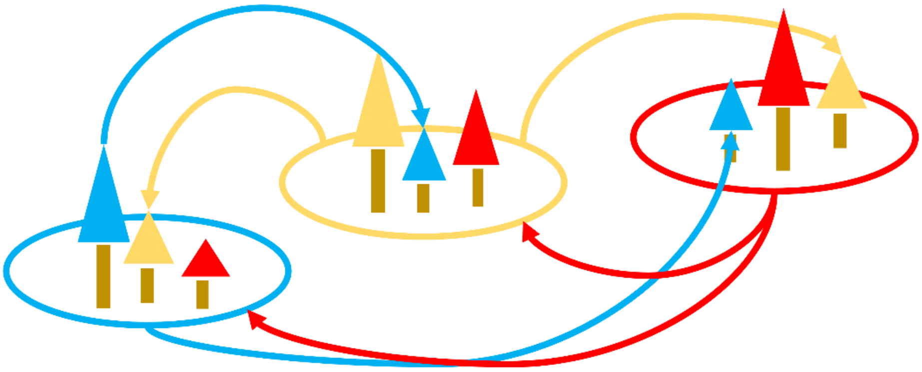
Mémoire pour le Diplôme de l'**Habilitation à Diriger des Recherches**

ΔTraitSDM: Species distribution models that account for local adaptation and phenotypic plasticity



MARTA BENITO GARZÓN

UMR Biodiversité, Gènes et Communautés
INRA - Université de Bordeaux

Université de Bordeaux, Ecole doctorale *Sciences et Environnements*

November 2018

SUMMARY

1. CURRICULUM VITAE

1.1. Professional trajectory and personal data

Place and date of birth: Madrid (Spain) 29/06/1977
Nationality: Spanish
Languages: Spanish (native), English, French and Italian (fluent)
Postal Address: Allée Geoffroy-St-Hilaire,
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1.1.1. Research profile

I have a background in biogeography, spatial ecology and ecological modeling. I started designing niche models to understand the present, past and future relationships of species ranges with climate, at a time when this approach was not yet very frequent. Later on, I moved to functional biogeography by incorporating the phenotypic variation (including ecophysiological limits and genetic adaptation components) of several traits into species distribution models. Recently, I started to work on a new research line focused on socio-ecosystems adaptation to climate change strategies, with special attention to assisted migration and biological invasions.

1.1.2. Professional trajectory and mobility

2016 – present: Chargée de recherché CR1 INRA (UMR BIOGECO)

2015 -2018: Idex "*Junior Chair*" - University of Bordeaux (UMR 1202 BIOGECO).

2012 – 2015: "*Marie Curie"* fellow (including 9 months of *maternity leave* and 4 months of *part time work*) - Centre International de Recherche sur l'Environnement et le Développement (CNRS - CIRED) and Université Paris-Sud, Orsay. 2014 – 2015 Visiting fellow at INRA Bordeaux (UMR 1202 BIOGECO).

2012 – 2013: CNRS postdoctoral position - Centre International de Recherche sur l'Environnement et le Développement (CNRS - CIRED) and Université Paris-Sud, Orsay.

2009 – 2012: "*Juan de la Cierva"* fellow (including 9 months of *maternity leave*) Centro de Investigaciones Forestales (CIFOR), Instituto Nacional de Investigación Agraria (INIA), Madrid, Spain.

2008: CNRS postdoctoral position - Université Paris-Sud, Orsay.

2006 – 2007: CNRS postdoctoral position - Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), Montpellier.

13.07.2006: Doctoral degree - Universidad Autónoma Madrid, Spain.

2003 – 2006: Postgraduate studies - Universidad Autónoma Madrid and Fondazione Bruno Kessler, Trento, Italy.

2002 – 2003: Research Assistant - Experimental Station of Arid Zones (EEZA, CSIC). Almeria, Spain.

2000 – 2002: Master of Science studies - Universidad Autónoma Madrid and Environmental Change Institute, Oxford, UK.

1995 – 2000: Undergraduate studies in Biology - Universidad Autónoma de Madrid, Spain.

1.1.3. Distinctions and awards

2015 : Idex "Junior Chair" - University of Bordeaux.

2012: "Marie Curie" Intra European Fellowship (FP7-PEOPLE-2012-IEF) - European Union.

2009: "Juan de la Cierva" postdoctoral fellowship - Spanish Ministry of Science and Education.

2007: European Science Foundation Grant to participate in the "ESF-JSPS, Frontier of Science Conference for Young Researchers: Climate Change" Nynäshamn, Sweden.

2006: European Doctorate

2003: National Research Grant for accomplishing the PhD (FPU) - Spanish Ministry of Science and Education.

1.2. Research Activity

1.2.1. Coordination of research projects (Principal Investigator)

2018 – 2019: EFPA Department – Accompagnement nouveau chercher. Project: Contribution of seed production to fitness of European beech across its distribution range. (11k€)

2015 – 2018: Idex Junior Chair. Project: *Ecological and economic assessment of forest community assembly mediated by climate change* (COMECO). (311k€)

2012 – 2015: Marie Curie Action. *Assisted migration of forests as a climate change economic mitigation strategy* (AMECO). (120k€).

1.2.2. Participation in research projects (duties)

2018 – 2022: B4EST Horizon2020 (50k€→ Task Leader)

2016 – 2020: GENTREE Horizon2020 « Optimizing the management and sustainable use of forest genetic resources in Europe » (50k€→ Task leader)

2016 – 2020: Regional project Aquitaine Athéné « Atténuation des effets du changement climatique sur la biodiversité et les services écosystémiques des forêts d'Aquitaine » (50k€→ Task Leader)

2016 – 2020: MicroMic Forecasting changes in microclimate and microbial diversity within tree canopies under climate change scenarios. Labex COTE (4k€)

2016 – 2020: CLIMO. Climate-Smart Forestry in Mountain Regions. COST Action, EU (→ National co-coordinator, MC Member).

2012 – 2015: AMTools. *Ecological and legal tools for the assisted migration of forests*. Agence Nationale de la Recherche (ANR).

2009 – 2012: TERRABITES. *Earth system science and environmental management*. COST Action, EU.

2008 – 2010: EVOLTREE. *Evolution of trees as drivers of terrestrial diversity*. EU Network of Excellence.

2003 – 2006: MARBOCLIM. *Modeling the past and future distributions of the Spanish forests under climate change*. Plan Nacional (corresponding to French ANR Blanc), Spanish Ministry of Science and Education.

1.2.3. Editorial duties

2018 - Associated Editor of Forest Systems *http://revistas.inia.es/index.php/fs/index*

1.2.4. Evaluation of Science

Referee for International Journals

Climatic Change, Diversity and Distributions, Ecography, Ecological Modelling, Ecological Informatics, Ecology, Ecological Applications, Evolutionary Applications, Global Change Biology, Global Ecology and Biogeography, Journal of Biogeography, Journal of Vegetation Science, Plant, Cell and Environment, PloSOne, Proceedings of the National Academy of Sciences, Quaternary Research, Regional Environmental Change.

Referee for International Science Agencies

2017 - Discovery Program of the Natural Sciences and Engineering Research Council of Canada (NSERC)

2016 – Comisión Nacional de Investigación Científica y Tecnológica of Chile (CONICYT)

1.2.5. Other research activities

2018: Member of the jury committee of the Master program: Science, Tecnologies, Santé (Mention Biodiversité, Ecologie & Evolution), Université de Bordeaux.

2016 - present: scientific animator of one of the Axis of research of BIOGECO (INRA).

2013: Co-organizer with Minh Ha-Duong, Juan Fernández Manjarrés and Nathalie Frascaria-Lacoste of a Special Session "*Decision making with incomplete data in forest adaptation to climate change*" for the first European Climate Change Adaptation Conference (ECCA; >700 participants), Hamburg, Germany.

2012 – present: Member **of 3 PhD committees**: Universidad Autónoma de Barcelona (Josep M. Serra Díaz and Universidad de Alcalá de Henares (Paloma Ruiz Benito), Universidad de Valladolid – INIA (María Jesús Serra Varela).

2010 – present: Seven invited seminars in Europe, Japan and the US.

2010: Co-organizer with Miguel A. Zavala of the COST workshop "*Terrestrial Ecosystems as Complex Adaptive Systems: how to integrate adaptive processes in response to disturbances into Dynamic Global Vegetation Models (DGVMs)?*" TERRABITES COST ES0805, Madrid.

1.3. Teaching activities

2012: Qualification to teach in French public universities. **N° de qualification: 12267231220**

2009 – present: Visiting lecturer in five under- and post- graduate courses (Universidad Autónoma de Madrid, Universidad de Alcalá, AgroParisTech, Université de Bordeaux, University of Helsinki)

2015 – present: I have supervised 4 Master students, 3 PhD students and 2 postdocs.

1.3.1. Supervision of students and young researchers

Master students

Juliette ARCHAMBEAU (2018). **Master 2** Sciences, technologies, santé (Université de Bordeaux). *Assessing background tree mortality of Pinus sylvestris and Fagus sylvatica in Europe from National Forest Inventories: methods comparison*. In collaboration with Paloma Ruiz Benito and Sophie Ratcliffe (University of Alcala de Henares, Spain). (Idex Junior Chair).

> Archambeau J, Ruiz-Benito P, Ratcliffe S, **Benito Garzón M**. New methods for predicting tree mortality at the continental scale. *In prep.*

Juliette ARCHAMBEAU (2017) *Driving factors of recent Scots pine mortality in European forests*. **Master 1** Sciences, technologies, santé (Université de Bordeaux). (Idex Junior Chair).

Gotzon BOUDOU-AGUIRRE (2017) *Testing community turnover in the Nouvelle-Aquitaine region under recent climate change.* **Master 2** Modélisation des Systèmes Ecologiques (MSE, Université de Toulouse). (Labex COTE).

> Contribution to the Chapter *Nouvelles forêts et nouvelles attentes* in – Le Treut H (Ed.) (2018) Anticiper les changements climatiques en Nouvelle-Aquitaine pour agir dans les territoires. Comité Scientifique Régional Acclimaterra. Editions Region Nouvelle-Aquitaine, 487pp.

Etienne CAMENEN (2015) *Understanding tree invasions under climate change: a modelling approach*. **Master 2** Modélisation des Systèmes Ecologiques (MSE, Université de Toulouse). (Labex COTE).

> Camenen E, Porte AJ, **Benito Garzón M** (2016). American trees shift their niches when invading Western Europe: Evaluating invasion risks in a changing climate. *Ecology and Evolution.* 6:7263–7275.

PhD students

Juliette ARCHAMBEAU (2018 – 2021) Comment définir l'aire de répartition des espèces à partir des mécanismes d'adaptation locale, de plasticité et de la structure des populations (« Bourse au mérite » University of Bordeaux). In co-supervision with Santiago Gonzalez Martinez.

Alexandre CHANGENET (2017-2020) Assessing the ecological and economic consequences of species turnover in French forests (Grant Region Aquitaine and Index Junior Chair from the University of Bordeaux). In co-supervision with Annabel Porte.

Homero GARATE ESCAMILLA (1017-2020) Modeling forest tree community turnover based on species' phenotypic variability and response to climate change (CONACTY Mexico). In co-supervision with Arndt Hampe.

> Gárate Escamilla H, Hampe A, Vizcaino Palomar N, Robson, MT, **Benito Garzón M**. Range-wide variation in local adaptation and phenotypic plasticity of fitness-related traits in *Fagus sylvatica* and their implications under climate change. *Submitted.*

Postdocs

Thibaut FREJAVILLE (2016-2019) Learning ecological and evolutionary processes from big databases: national forest inventories and common gardens (Idex Junior Chair)

> Fréjaville T, Fady B, Kremer A, Ducousso A, **Benito Garzón, M**. Inferring phenotypic plasticity and local adaptation to climate across tree species ranges using forest inventory data. *In review*

> Fréjaville T, Fady B, Kremer A, **Benito Garzón, M**. Climate adaptation lags in European forest trees. *Submitted*

Fréjaville T, **Benito Garzón, M**. The EuMedClim dataset: time series (1901-2017) of 1-km resolution climate grids for Europe and Mediterranean basin. *Frontiers in Ecology and Evolution.*

Database repositories:

EuMedClim (2018) http://gentree.data.inra.fr/climate

Natalia VIZCAINO PALOMAR (2016-2019) The role of phenotypic plasticity under climate change (Idex Junior Chair & GENTREE)

Vizcaíno Palomar N, Fady B, Raffin A, Mutke S, **Benito Garzón, M**. Is phenotypic plasticity higher for those populations that have experienced higher climatic variability in the last century? *In review.*

Vizcaíno Palomar N, **Benito Garzón M,** Alía R, Giovanelli G, Huber G, Mutke S, Pastuszka P, Raffin A, Sbay H, Seho M, Vautier D, Fady B "Geographic variation of tree height of three pine species (*Pinus nigra* Arn., *P. pinaster* Aiton and *P. pinea* L.) gathered from common gardens in Europe and North-Africa. *In review*

Database repositories:

Vizcaíno-Palomar N, **Benito Garzón M,** Alia R, Pastuszka P, Raffin A., Sbay H, Fady B (2018) Geographic variation of tree height of *Pinus pinaster* Aiton gathered from common gardens in Europe and North-Africa. https://doi.org/10.5281/zenodo.1242980

Vizcaíno-Palomar N, **Benito Garzón M,** Alia R, Guiovanelli G., Huber G, Seho M, Fady B (2018) Geographic variation of tree height of *Pinus nigra* Aiton gathered from common gardens in Europe and North-Africa. https://doi.org/10.5281/zenodo.1242960

Vizcaíno-Palomar N, **Benito Garzón M,** Mutke S., Vauthier D., Fady B (2018) Geographic variation of tree height of *Pinus pinea* Aiton gathered from common gardens in Europe and North-Africa. https://doi.org/10.5281/zenodo.1242991

1.3.2. Member of PhD committees

2017 - *Integrating infra-specific variation of Mediterranean conifers in species distribution models. Applications for vulnerability assessment and conservation*. M.J. Serra Varela. University of Valladolid, Spain.

2015 - *Conifer responses to environment at local and regional scales: the role of intraspecific phenotypic variation*. Natalia Vizcaino Palomar. Universidad de Alcalá de Henares, Spain.

2013 – *Patterns and drivers of Mediterranean forest structure and dynamics: theoretical and management implications*. Paloma Ruiz Benito. Universidad de Alcalá de Henares, Spain. External reporter.

2012 - *Applying correlative ecological niche models to global change studies*. Josep Serra Diaz. Universitat Autonoma de Barcelona, Spain.

1.4. Scientific contribution

1.4.1. Overview

o 23 articles published in journals of the ISI Web of Science (including *Ecology Letters, Global Ecology and Biogeography, Nature Scientific Data*): 13 as first author and 2 as last author. Google scholar citations by 05.11.2018 =1233, h index = 13.

o 7 further articles under review in journals of the ISI Web of Science (1 as first author and 3 as last author).

o 12 articles in other peer reviewed journals.

o 7 book chapters.

o 5 databases published: Zenodo and INRA repositories.

o Associated editor of *Forest Systems* journal.

o 34 contributions to international conferences (6 of them as invited speaker; 1 as keynote speaker) in US, Europe, Canada & Japan.

1.4.2. Peer reviewed publications

23. Fernández-Manjarrés J. F., Ruiz-Benito P, Zavala M.A., Camarero J.J., Pulido F, Proença V, Navarro L, Sansilvestri R., Granda E., Marqués L., Temunovic M, Bertelsmeier C., Drobinski J.P., Roturier S., **Benito Garzón M**., Garcia de Cortazar-Atauri I., Simon L., Dupas S., Levrel H., Sautier M. (2018) Forest adaptation to climate change along steep ecological gradients: The case of the Mediterranean-temperate transition in South-Western Europe. *Sustainability* 10: 3065

22. Robson T.M.*, **Benito Garzón M**.*, BeechCOSTe52 Database Consortium. (2018) Phenotypic trait variation measured on European genetic trials of *Fagus sylvatica* L. *Scientific Data* 5: 180149. **Joint first author contribution. Press release:* [*http://presse.inra.fr/Communiques-de-presse/Base-de-donnees-hetres*](http://presse.inra.fr/Communiques-de-presse/Base-de-donnees-hetres)

21. Fréjaville T, **Benito Garzón, M**. (2018) The EuMedClim dataset: time series (1901-2017) of 1-km resolution climate grids for Europe and Mediterranean basin. *Frontiers in Ecology and Evolution* 6: 3.

20. Wan Q., Zheng Z., **Benito Garzón, M**., Petit R.J. (2018) Inconsistent interspecific and intraspecific differentiation of climate envelopes in a subtropical tree. *Journal of Plant Ecology*

19. **Benito Garzón, M.***, González Muñoz N.*, Fernández-Manjarrés, J. F., Wigneron J.P., Moisy C., Delzon S. (2018) The legacy of water deficit on populations having experienced negative hydraulic safety margin. *Global Ecology and Biogeography* 27: 346-356. **Joint first author contribution.*

18. **Benito Garzón, M**., Fady B., Davi H, Vizcaino-Palomar N., Fernández-Manjarrés, J. F. (2018) Trees on the move: Using decision theory to compensate for climate change in forest social-ecological systems. *Regional Environmental Change* 18: 1427-1437.

17. Stojnić S., Suchocka M., **Benito-Garzón M.**, Torres-Ruiz J.M., Cochard H., Bolte A., Cocozza C., Cvjetković B., de Luis M., Martinez-Vilalta J., Ræbild A., Tognetti R. and Delzon S. (2018) Variation in xylem vulnerability to embolism in European beech marginal populations. *Tree Physiology* 38: 173-185.

16. Vizcaíno-Palomar, N., Ibáñez, I., **Benito-Garzón, M**., González-Martínez, S. C., Zavala, M. A., Alía (2017). Climate and population origin shape pine tree height-diameter allometry. *New Forests, 48* (3), 363-379.

15. Camenen, E., Porté, A. J., **Benito Garzón, M**. (2016). American trees shift their niches when invading Western Europe: evaluating invasion risks in a changing climate. *Ecology and evolution, 6* (20), 7263-7275.

14. **Benito Garzón, M**., Fernández-Manjarrés, J. F. (2015). Testing scenarios for Assisted Migration of Forest Trees in Europe. *New Forests, 46*, 979-994.

13. **Benito Garzón, M.,** Leadley, P. W., Fernández-Manjarrés, J. F. (2014). Assessing global biome exposure to climate change through the Holocene - Anthropocene transition. *Global Ecology and Biogeography, 23*, 235-244.

12. Valladares, F., Matesanz, S., Araujo, M. B., Balaguer, L., **Benito Garzón, M.**, Cornwell, W., Gianoli, E., Guilhaumon, F., van Kleunen, M., Naya, D. E., Nicotra, A. B., Poorter, H., Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters, 17*, 1351-1364.

11. **Benito Garzón, M.,** Ha-Duong, M., Frascaria-Lacoste, N., Fernández-Manjarrés, J. F. (2013). Extreme climate variability should be considered in forestry-assisted migration. *Bioscience, 63*, 317.

10. **Benito Garzón, M.,** Ruiz-Benito, P., Zavala, M. A. (2013). Inter-specific differences in tree growth and mortality responses to environmental drivers determine potential species distribution limits in Iberian forest. *Global Ecology and Biogeography, 22*, 1141-1151.

9. **Benito Garzón, M.**, Ha-Duong, M., Frascaria-Lacoste, N., Fernández-Manjarrés, J. F. (2013). Habitat restoration and climate change: dealing with climate variability, incomplete data and management decisions with tree translocations. *Restoration Ecology, 21*, 30-36.

8. **Benito Garzón, M.**, Alia, R., Robson, T. M., Zavala, M. A. (2011). Intraspecific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography, 20*, 766-778.

7. Calleja, J. A., **Benito Garzón, M.**, Sáinz Ollero, H. (2009). A Quaternary perspective on the conservation prospects for the Tertiary relict tree *Prunus lusitanica* L. *Journal of Biogeography, 36*, 487-498.

6. Sánchez de Dios, R., **Benito Garzón, M.**, Sáinz Ollero, H. (2009). Present and future

extension of the Iberian Submediterranean territories as determined from the distribution of marcescent oaks. *Plant Ecology, 204*, 189-205.

5. **Benito Garzón, M.**, Sánchez de Dios, R., Sáinz Ollero, H. (2008). The evolution of the *Pinus sylvestris* L. area in the Iberian Peninsula from the last maximum glacial (21000BP) to 2100 under climate change. *The Holocene* 18: 705-714.

4. **Benito Garzón, M.**, Sánchez de Dios, R., Sáinz Ollero, H. (2008). Effects of climate change on the distributions of Iberian forests. *Applied Vegetation Science* 11: 169-178.

3. **Benito Garzón, M.**, Sánchez de Dios, R., Sáinz Ollero, H. (2007). Predictive modelling of tree species distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-Holocene. *Ecography, 30*, 120-134.

2. Sánchez de Dios, R., **Benito Garzón, M.**, Sáinz Ollero, H. (2006). Hybrid zones between two European oaks: A plant community approach. *Plant Ecology, 187*, 109-125.

1. **Benito Garzón, M**., Blazek, R., Neteler, M., Sánchez de Dios, R., Sáinz Ollero, H., Furlanello, C. (2006). Machine learning models for predicting species habitat distribution suitability: An example with *Pinus sylvestris* L. for the Iberian Peninsula. *Ecological Modelling, 3-4*, 383-393.

1.4.3. Articles under review in peer-reviewed journals

7. Sansilvestri R, Cuccarollo M, Frascaria-Lacoste N, **Benito Garzón M,** Fernandez Manjarrés J What types of capital for sustainable transitions in forest-human systems?

6. Ruiz-Benito P, Vacchiano G, Lines ER, Reyer CPO, Ratcliffe S, Morin X, Hartig F, Mäkelä A, Yousefpour R, **Benito Garzón M**, Morales-Molino C, Camarero JJ, Jump AS, Lehtonen A, Ibrom A, Owen HJF, Zavala MA. Achievements and challenges of data available to parameterise current models and assess European forest vulnerability to climate change

5. Archambeau J. Ruiz Benito P, Ratcliffe S, Changenet A, Frejaville T & Benito **Garzón** M Driving factors of recent Scots pine mortality in European forests.

4. **Benito Garzón M**, Robson TM, Hampe A. ΔTraitSDM: Species distribution models that account for local adaptation and phenotypic plasticity.

3. Gárate Escamilla H, Hampe A, Vizcaíno Palomar N, Robson TM & **Benito Garzón M**. Range-wide variation in local adaptation and phenotypic plasticity of various fitness-related traits in *Fagus sylvatica*.

2. Vizcaíno-Palomar N, **Benito Garzón M,** Fady B. Geographic variation of tree height of three pine species (*Pinus nigra* Arn., *P. pinaster* Aiton and *P. pinea* L.) gathered from common gardens in Europe and North-Africa.

1. Fréjaville T, Fady B, Kremer A, Ducosso A, **Benito Garzón, M**. Inferring phenotypic plasticity and local adaptation to climate across tree species ranges using forest inventory data

1.4.4. On line databases

5. Robson TM, **Benito Garzón M**. et al. (2018) Beech COST e52 Database. DOI:10.5281/zenodo/1205431; https://zenodo.org/record/1205431

4. EuMedClim (2018) http://gentree.data.inra.fr/climate

3. Vizcaino-Palomar N, **Benito Garzón M,** Alia R, Pastuszka P, Raffin A., Sbay H, Fady B (2018) Geographic variation of tree height of *Pinus pinaster* Aiton gathered from common gardens in Europe and North-Africa. https://doi.org/10.5281/zenodo.1242980

2. Vizcaino-Palomar N, **Benito Garzón M,** Alia R, Guiovanelli G., Huber G, Seho M, Fady B (2018) Geographic variation of tree height of *Pinus nigra* Aiton gathered from common gardens in Europe and North-Africa. https://doi.org/10.5281/zenodo.1242960

1. Vizcaino-Palomar N, **Benito Garzón M,** Mutke S., Vauthier D., Fady B (2018) Geographic variation of tree height of *Pinus pinea* Aiton gathered from common gardens in Europe and North-Africa. https://doi.org/10.5281/zenodo.1242991

1.4.5. Books and other publications

7. Le Treut H (Ed.) (2018) Anticiper les changements climatiques en Nouvelle-Aquitaine pour agir dans les territoires. Comité Scientifique Régional Acclimaterra. Editions Region Nouvelle-Aquitaine, 487pp.

6. Ruiz-Benito P, **Benito Garzón M,** García-Valdés R, Zavala MA (2015) Aplicación de Modelos de distribución de Especies para analizar los efectos del cambio climático. Oficina Española de Cambio Climático. Ministerio de Agricultura, Alimentación y Medio Ambiente.

5. Fernández-Manjarrés JM, Benito Garzón M (2014) El debate de la migración asistida en los Bosques de Europa Occidental. Oficina Española de Cambio Climático. Ministerio de Agricultura, Alimentación y Medio Ambiente.

4. Ruiz Benito P, **Benito Garzón M**, García Valdés R, Gómez Aparicio L., Zavala MA (2013). Estructura y dinámica del bosque Mediterráneo frente al cambio climático: aplicación de modelos en ecología. En: Aplicaciones de modelos ecológicos en la gestión de recursos naturales. En: Blanco, J.A. (ed.), Aplicaciones de modelos ecológicos a la gestión de recursos naturales, pp. 77-107. Omnia Science, Barcelona, España.

3. Ruiz Benito P, **Benito Garzón M**, García Valdés R, Gómez Aparicio L, Purves DW, Ojeda E, Aragón CF, Alía R, Aunón FJ, Zavala MA. 2011. Observatorio de la

sostenibilidad en España: zonas forestales. (Sustainability in Spain: forests). Ed. Spanish Ministry of Science.

2. Domínguez F, **Benito Garzón M,** Sainz H, Moreno JC, Albert MJ (2009) *Vella pseudocytisus* L. subsp. *paui* Gómez Campo. In Poblaciones en Peligro: Viabilidad Demográfica de la Flora Vascular Amenazada de España.

1. Maldonado J, **Benito Garzón M**, Sánchez de Dios, Sainz Ollero H. (2002) Evolución reciente de las áreas de los bosques esclerófilos ibéricos. Cambios deducidos a partir de la cartografía forestal. In La regeneración Natural del Bosque Mediterráneo en la Península Ibérica. Ed.: J. Charco (ARBA y DGCONA).

1.4.6. Invited conferences

12. **Benito Garzón M** (2019) Fitness, phenotypic variation and species ranges. University of Helsinki Organismal and Evolutionary Biology seminars. « Invited seminar».

11. **Benito Garzón M** (2017) Why do we need to incorporate phenotypic variation into species distribution models? MEDECOS - AEET Human-driven scenarios for evolutionary and ecological changes. Sevilla, Spain. « Key-note lecture ».

10. **Benito-Garzón M**, Fady B, Vizcaíno-Palomar N, Fernández-Manjarrés J. (2015). Integration of provenance tests and National Forest Inventories to account for intraspecific variation in species distribution models. Annual meeting of the Ecological Society of America (ESA). Baltimore, USA. « Invited oral presentation ».

9. **Benito-Garzón M.** (2015). Journée Brainstorming INRA/ONF "Adaptation des forets au changement climatique". 1-2 July Campus ONF à Velaine en Haya, Nancy. « Invited oral presentation ».

8. **Benito-Garzón M,** Fernández-Manjarrés J. (2014) Using climate anomalies and bioclimatic niche models to define vulnerabilities and assist provenance choice for assisted migration programs. Workshop: "From science to practice: the contribution of projects TipTree and AMTools to guiding better forest survival and regeneration under Global Change scenarios", Paris, France.

7. **Benito-Garzón M**, & Fernández-Manjarrés JF. (2014) Testing scenarios for Assisted Migration of Forest Trees in Europe. Restoring Forests: what constitutes success in the 21th century? Lafayette, Indiana, U.S.A. « Oral presentation ».

6. Vizcaíno-Palomar N, Ibáñez I, **Benito-Garzón M,** Martinez-Gonzalez SC, Zavala MA, Alia R (2014) Predicting changes in aboveground allometry in four pine species in response to climate change: implications in restoring forests. Restoring Forests: what constitutes success in the 21th century? Lafayette, Indiana, U.S.A. 14 - 16 October. « Oral presentation ».

5. **Benito-Garzón M,** Ha-Duong M, Frascaria-Lacoste N, F & Fernández-Manjarrés JF.

(2013) Decision making with incomplete data and uncertainty in Ecology: the case of Assisted Migration of forests. European Climate Change Adaptation Conference (ECCA). Hamburg. 18-20 March, 2013 « Oral presentation ».

4. **Benito-Garzón M**. 2013. Workshop on forest modeling and climate change in the Spanish context. Biodiversity and Landscape Ecology Lab. Solsona, Spain. « Invited oral presentation ».

3. **Benito-Garzón M**, Fernández-Manjarrés J. 2012. Modeling assisted migration of forests in France. Adaptive trait seminar. CESAB, Aix-en-Provence, France. « Oral presentation ».

2. **Benito-Garzón M**, Zavala MA. 2011. Phenotypic variability: the missing ingredient in modeling species responses to a changing world. Madrid. National History Science Museum, Madrid. « Invited oral presentation ».

1. **Benito-Garzón M**, Alía R, Robson TM, Zavala MA. 2010. Intraspecific variability and plasticity influence potential tree species under climate change. Eco-evolutionary approaches to understanding and predicting the response of species range to climate change. A Joint workshop of bioDISCORVERY and bioGENESIS, DIVERSITAS Hakozaki, Kyushu University, Japan. « Invited oral presentation ».

2. ACTIVITY REPORT

I am a spatial ecologist and my research focuses on understanding ecological processes across large environmental gradients. My background is in macroecology and biogeography and its applications; it comprises three lines of research: 1) Climate driven range dynamics of species and biomes, with special attention to ecotones; 2) Traits and processes across species ranges, with special focus on tree mortality and growth regarding the traits, and phenotypic plasticity and local adaptation regarding the processes; 3) Management, conservation and applications of ecological models to the real world.

During my PhD I started to develop my interest in modeling the effects of climate change on trees. My subsequent work brought together several related fields from functional biogeography and species distribution models to population genetics and, most recently, to management strategies for adapting forests to a changing climate and concomitant biological invasions. After my PhD dissertation I obtained a first postdoctoral contract from the CNRS (CEFE and Université Paris-Sud) that allowed me to apply my model to conservation biology (Calleja *et al.*, 2009) and genetics (Benito Garzón *et al.*, 2011). In particular, we could demonstrate that the conservation status of some so-called Tertiary relicts (i.e., species adapted to climates that dominated Europe before the Pleistocene) actually depends more on human land use than on climate (Calleja *et al.*, 2009). In the following, I will describe the three research lines that I develop. They relate mainly to my two awarded postdoctoral fellowships: *Juan de la Cierva* at INIA (Spain) and *Marie Curie* and CNRS contract at Université Paris-Sud, CIRED and my work since my recruitment as CR1 (2016) in BIOGECO (France). Since 2015, I have the support of the Chair Junior from the Idex Program of the University of Bordeaux, which has been a strong support to settle my own research team within BIOGECO. Currently, I am leading one major research project (IdEx Chair, University of Bordeaux: 2015-2018) and a small targeted project to help recently-recruited researchers at INRA (BeechSeed: 2018-2019) and also have major responsibilities as task leader in two EU H2020 (GenTree and B4EST) and one Regional (Athéné) research project, and I am part of the advisory board of the EU Interreg Central Europe program SusTree, which assures good communication between SusTree and GenTree, both similar projects funded by the EU. The framework of these three European projects allows me to coordinate the compilation of tree provenance trials in Europe, which has allowed me test different hypotheses regarding the adaptation and plasticity of fitness-related traits across species ranges. I also am the French national co-coordinator of the COST Action CLIMO. I currently supervise two postdocs and three PhD students.

2.1. Environment, funding and collaborations

Here I explain the funding strategies and main collaborators in the three research topics that I develop.

1) Climate driven range dynamics of species and biomes, with special attention to ecotones

This topic has been mainly founded by the Idex, *Region Project Athéné* and the Labex COTE. Gotzon Boudou-Aguirre (Master 2 University of Toulouse) analyzed the ecotone between Mediterranean and temperate biomes in Nouvelle-Aquitaine. Alexandre Changenent (PhD student; 2017- 2020) is currently focused on the analysis of the ecotones in Europe (Mediterranean- Temperate, Temperate-Boreal) and the role of invasive trees using demographic traits issue of 6 National Forest Inventories from Finland to Spain.

Main collaborators: Sophie Ratcliffe (Universidad de Alcala), Paloma Ruiz Benito (Universidad de Alcala), Juan Fernandez Manjarres (CNRS Universite Paris-sud), Annabel Porté (INRA BIOGECO).

2) Traits and processes across species ranges, with special focus on tree mortality and growth regarding the traits and phenotypic plasticity and local adaptation regarding the processes

This topic includes the study of mortality across species ranges and the study of the role of phenotypic plasticity and local adaptation across common gardens. The analysis of mortality includes the works of M1 & M2 of Juliette Archambeau (2017 – 2018) that was funded by the *Idex Junior Chair*.

The analysis of plasticity and local adaptation involves one PhD student (Homero Garate Escamilla) and two postdocs (Natalia Vizcaino Palomar and Thibaut Fréjaville) and is funded by the *Idex Junior Chair* from the University of Bordeaux and *H2020 GenTree & B4EST*.

Main collaborators: Bruno Fady (INRA – Avignon), Sylvain Delzon (INRA – Bordeaux), Arndt Hampe (INRA - BIOGECO), T. Matthew Robson (University of Helsinki, Finland).

3) Management, conservation and applications of the theories and models to the real world.

In this applicative part of my research I transfer the models to propose management and conservation tools. It was mainly funded by the ANR AMTools, AMECO Marie Curie project and *Idex Junior Chair*.

Main collaborators: Juan Fernandez Manjarrés (University of Paris Sud, CNRS), Luc Doyen and Lauriane Mouyset (CNRS, University of Bordeaux), Michele Bozzano (EFI, Bioversity International).

2.2. Chapter 1. Introduction – ΔTraitSDM: Species distribution models that account for local adaptation and phenotypic plasticity[1]

Understanding species ranges has always attracted the attention of ecologists, and even more given our awareness that the persistence of species ranges depends on the tolerance and adaptive capacity of populations to conditions created by a changing climate. As a consequence, emerging modelling approaches here assembled as ΔTraitSDM, attempt to explain species distribution ranges based on the phenotypic plasticity and local adaptation of fitness-related traits measured across large geographical gradients. The collection of intraspecific traits measured in common gardens spanning broad environmental clines has promoted the development of these new models; firstly in trees but now rapidly expanding to other organisms. Here we explain, harmonize and review the main ecological improvements arising from the new generation of models that, by including trait variation over geographical scales, are able to give new insights into future species ranges. Overall, ΔTraitSDM predictions give a less alarmist message than previous models of species distribution under new climates, showing that phenotypic plasticity should help some plant populations to persist under climate change. The development of ΔTraitSDM opens a new perspective to analyse intra-specific multi-trait variation, with the rationale that trait co-variation, and hence fitness, can change across geographical gradients and new climates.

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[1] Benito Garzón M, Robson TM, Hampe A. (in review) ΔTraitSDM: Species distribution models that account for local adaptation and phenotypic plasticity

2.2.1. *ΔTraitSDM: context*

The observed impact of contemporary climate warming on patterns of species migration and range shift has created a high demand for forecasts of biodiversity changes. Species distribution models (SDM) are a widely-used tool for generating hypotheses about the potential consequences of climate changes on the natural distribution of species (Urban, 2015). SDM are correlational models of low structural complexity that rely on the statistical relationship that exists between species' occurrence and local climate. However, these models have commonly been criticized for relying on oversimplistic assumptions and neglecting critical biological processes involved in species' response to a rapidly changing environment (Fordham *et al.*, 2018). Several mechanistic modelling approaches have been developed over the past years to better account for key ecological processes such as species' dispersal ability, (meta-)population demography and dynamics, and the role of different biotic interactions (Wisz *et al.*, 2013; Normand *et al.*, 2014). These refined approaches have considerably improved our understanding of how climate warming could drive changes in the distributions of species and the abundance of populations across the range. However, very few models have to date considered a further key dimension in the response of populations to rapid environmental change: phenotypic variation in functional traits and its consequences for fitness (Valladares *et al.*, 2014; Roches *et al.*, 2018). Here, we review recent developments in this emerging field and develop a formal framework to unify different approaches that consider phenotypic trait variation under a common header for which we propose the term ΔTraitSDM.

Species ranges are constrained by the environmental conditions that local populations encounter, and they are modulated by the biological mechanisms that allow these populations to deal with environmental changes. Under rapid climate change, populations are expected to extirpate; to migrate tracking climate (Brito-Morales *et al.*, 2018); or to persist through phenotypic plasticity and evolutionary adaptation (Valladares *et al.*, 2014; Des Roches *et al.*, 2018), the two biological mechanisms at the basis of ΔTraitSDM. Phenotypic plasticity refers to the capacity of one genotype to render different phenotypes across environmental gradients, giving individual organisms the flexibility to rapidly react to environmental changes (Nicotra *et al.*, 2010). Evolutionary adaptation involves selection acting on heritable traits and that result in fitness differentials leading to a predominance of individuals with high performance within their local environment (Savolainen *et al.*, 2013). Phenotypic plasticity and local adaptation are ubiquitous in natural populations, and their interplay shapes the patterns of geographical variation in phenotypic traits across the species range (Savolainen *et al.*, 2013; Valladares *et al.*, 2014; Roches *et al.*, 2018). Range-wide surveys of intra-specific trait variation exist for numerous species worldwide. However, few studies have been able to tease apart these two underlying mechanisms and to identify their respective roles for fitness over large environmental gradients (Mclean *et al.*, 2014; Richardson *et al.*, 2017; Macdonald *et al.*, 2018). Until recently, a poor understanding of the role of phenotypic plasticity and local adaptation in shaping species ranges has critically limited attempts to anticipate how these mechanisms will drive the performance of populations under new climates (Des Roches *et al.*, 2018). This is now changing thanks to the increasing availability of data from common-garden and reciprocal-transplant experiments established along large environmental gradients (Robson *et al.*, 2018), for which reaction norms have been measured to quantify phenotypic variation of given populations across the species range. These data are fundamental for the development of ΔTraitSDM, emerging models that quantify local adaptation, phenotypic plasticity and their interaction across species ranges to get reliable predictions of populations' and species' persistence under new climates.

The dependence of ΔTraitSDM on extensive common-garden experiments that allow reaction norms across large environmental gradients to be estimated explains why these models were first developed in forest research (Rehfeldt *et al.*, 1999). Driven by the wish to identify suitable material for afforestation, common-garden experiments with many thousands of trees have been established and monitored over the past decades for a series of economically-important forest tree species. It is hence not surprising that early ΔTraitSDM based on the role of population differentiation in tree height mostly addressed management-related questions (Rehfeldt *et al.*, 1999). Since then, ΔTraitSDM have been expanded to more broadly consider how phenotypic plasticity and local adaptation affect projections of future species ranges (O'Neill *et al.*, 2008; Benito Garzón *et al.*, 2011; Oney *et al.*, 2013; Sáenz-Romero *et al.*, 2017; Rehfeldt *et al.*, 2018). During the last few years, the use of ΔTraitSDM has also extended to plants other than forest trees with the inception of large-scale experiments designed to separate local adaptation from phenotypic plasticity under controlled environmental conditions (Richardson *et al.*, 2017).

2.2.2. *ΔTraitSDM: traits, reaction norms, fitness and species ranges*

To account for phenotypic trait variation, ΔTraitSDM capture reaction norms of different provenances (i.e., populations from a specific geographic location) that are planted together in series of common-gardens across the species range (Figure 1). The rationale underlying this approach is that higher fitness implies a higher probability of population persistence in the local environment. To explain the relationship between trait variation and fitness in ΔTraitSDM, we can make use of SDM as baseline models: in SDM, the occurrence of a species in a given location is implicitly related to its survival capacity under certain climatic conditions with fitness represented as binary value (1 = maximum fitness: survival, and 0 = minimum fitness: no survival). In ΔTraitSDM, the binary information on species occurrence is replaced with empirical observations of fitness-related phenotypic traits of controlled genetic origin. This allows ΔTraitSDM to keep the statistical simplicity of SDMs, while (i) making an explicit, empirically grounded link with fitness-related traits; (ii) splitting the phenotypic variation of target traits into the components of local adaptation (i.e., related to the climate of origin of the provenance) and of phenotypic plasticity (i.e. related to the climate at the common-garden); and (iii) combining multiple traits and assessing their co-variation across species ranges (we propose the term multi-trait ΔTraitSDM for these approaches).

Following this rationale, ΔTraitSDM are developed in three steps (Figure 1) that are described in the following sections.

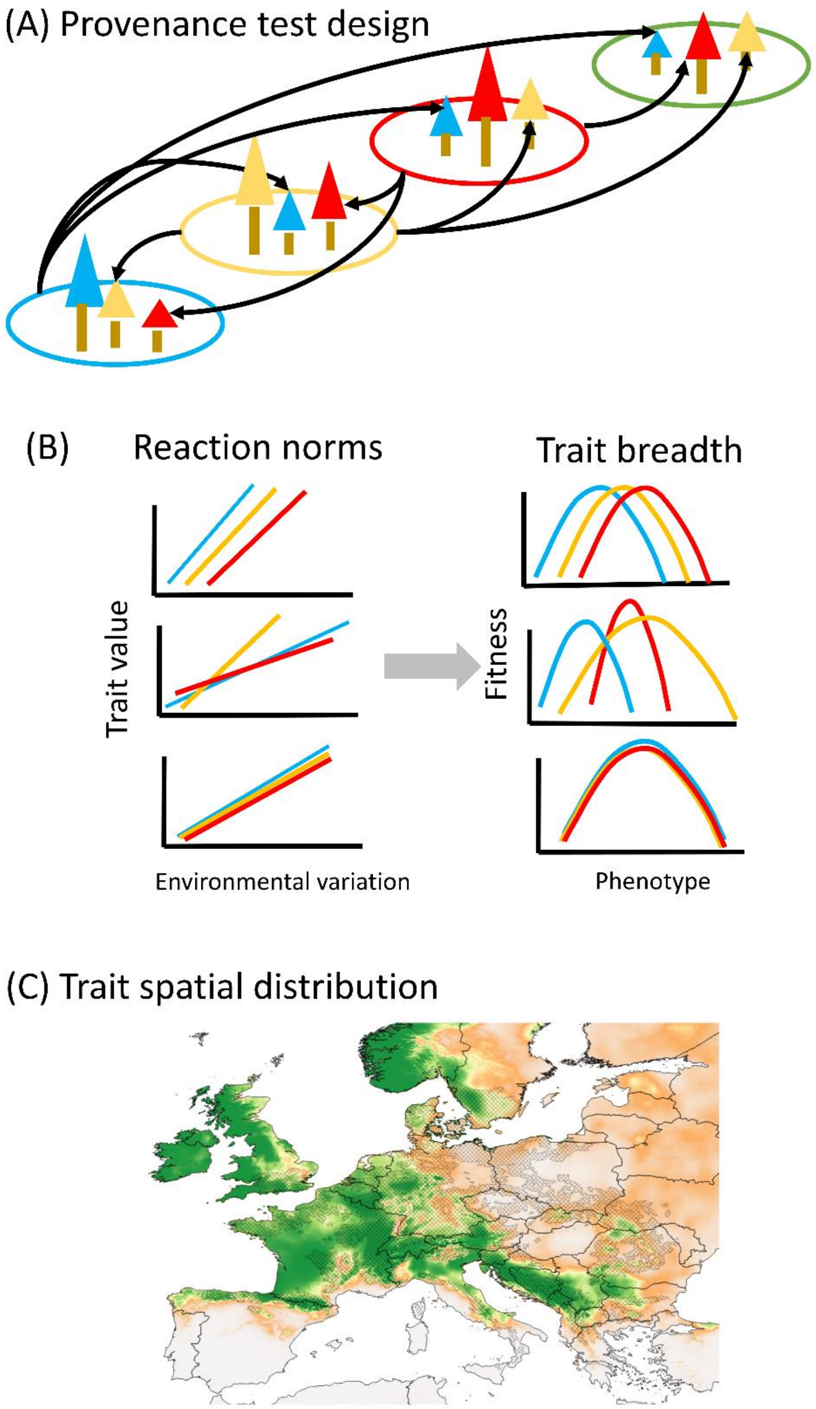


Figure 1. Conceptual framework of ΔTraitSDM: A) Experimental design in common garden networks across different climates (coloured oval shapes), where trees originating from different provenances (indicated by different colours: blue, red and yellow trees). Tree performance is represented by tree size; B) The graphics of the left represent different possible reaction norms built upon different provenances (indicated by colours) across common gardens (left graphics); the correspondent graphics on the right represent the transformation of reaction norms into trait breadth (i.e. the relationship between the phenotype and the fitness); C) Spatial prediction of a given fitness-related trait. The example shows the output of a ΔTraitSDM for *Fagus sylvatica* based on tree survival (adapted from Gárate Escamilla et al. under review) estimated from the BeechCOSTe52 network of common gardens (Robson *et al.*, 2018).

Gathering phenotypic trait variation from common gardens across large environmental gradients

ΔTraitSDM are based on trait measurements recorded in thoroughly replicated common gardens with many provenances to capture environmental variation across the species range (Figure 1A). The choice of a phenotypic trait is based on its putative relationship with fitness, defined in this context by the capacity of individuals to survive (survival success) and to contribute to the next generation (reproductive success). To date, the traits most commonly considered by ΔTraitSDM are those related to growth, spring phenology and mortality. Ecophysiological traits such as photosynthesis (Drake *et al.*, 2017; Patterson *et al.*, 2018), wood density (Díaz *et al.*, 2016), and xylem resistance to embolism (Anderegg *et al.*, 2016; Benito Garzón *et al.*, 2018) can affect demography and phenology and have a proven relationship with fitness across species ranges. Hence, they, are good candidates to be integrated in ΔTraitSDM when more information at the intra-specific level becomes available.

Integration of reaction norms in a unified model.

Reaction norms are calculated by regressing trait values against the climates of the provenance sites and the common gardens (Figure 1B). Regressions are based on the rationale that the climatic conditions that occurred at the location where the seed originated are related to local adaptation of the population, whereas the climatic conditions that occurred at the common garden since the time of its plantation are related to the acclimation response of phenotypic traits to climate, i.e. phenotypic plasticity (Leites *et al.*, 2012). Two regression methods are typically used to calculate trait reaction norms across species ranges: statistical models such as universal transfer functions or linear mixed-effect models; and machine learning techniques such as random forests or artificial neural networks. Universal transfer functions first fit one equation by provenance and then scale up to all experimental sites in a stepwise process (O'Neill *et al.*, 2008). Linear mixed-effect models combine the provenance and the site effect in a single equation, while including random effects that control for differences among experimental sites that are not related to climate (e.g. soil characteristics) (Leites *et al.*, 2012). Machine learning models are characterised by a greater flexibility as they can use any combination of predictors (i.e., several environmental drivers with complex non-linear relationships among them); they have a higher predictive power than statistical techniques but do not provide any form of equation. Hence, machine-learning approaches are an interesting option when the complexity of the combination of predictors prevents statistical convergence of other models (Benito Garzón *et al.*, 2011). The most widespread models are linear mixed-effect models because of their flexibility and capacity to account for the experimental design of common gardens as a random effect.

For linear mixed-effect models, the equation describing the regression between traits and environmental drivers in ΔTraitSDM takes the general form:

$$T_1 = a_0 + b_1\, CP + b_2\, CS + b_3\, CP \times CS + \beta + \delta + \varepsilon \qquad \text{(equation 1)}$$

Where T_1 is the trait value, a_0 represents the slope, b_1 , b_2 and b_3 are the coefficients of the regression, δ *is* the random effect controlling for variation arising from the common garden experimental design, and ε is the model error. *CP* represents the climatic variables characterizing the provenances, and *CS* the climatic variables characterizing the planting site. $CP \times CS$ represents the interaction between the climate of the provenance sites and those of the common garden sites. β can include model co-variates if needed.

Equation 1 allows us to quantify that part of the variance attributable to the genetic effect of each provenance (b_1), to the phenotypic plasticity (b_2) and the interaction between them (b_3) representing the genetic x environment effect.

Spatial prediction of phenotypic traits.

In addition to quantifying the plastic and genetic components of phenotypic trait variation, ΔTraitSDM can also be used to generate spatial projections of this trait variation under current or future climate scenarios using the fitted equation relationship with climate (equation 1, Figure C). Because traits and their relation with fitness can change across climatic gradients, projections are largely dependent on the trait used. Overall, higher values of fitness-related traits would be expected to correspond to species occurrence (Chakraborty *et al.*, 2018), but it depends on the trait used. For instance, traits related to reproduction would probably be more relevant near the leading range edge where colonization events and population growth prevail, whereas traits related to drought resistance would be more relevant near the trailing range edge (Hampe & Petit 2005).

2.2.3. *What can we learn from ΔTraitSDM?*

ΔTraitSDM are new and have been developed for very different purposes, therefore it is difficult to assess their contribution to understand phenotypic plasticity and local adaptation patterns across large gradients, and their implications for species ranges under current and future conditions. Two major messages emerge from examining the outputs of existing ΔTraitSDM, and from comparing them with SDM outputs as baseline models, for the very few studies that to date have explicitly done this (Table 1; Figure 2): (i) phenotypic plasticity is the most important component of intra-specific variation in demographic and phenological traits, and (ii) predictions using ΔTraitSDM generally depict a less pessimistic future for species ranges than forecasts based on SDM.

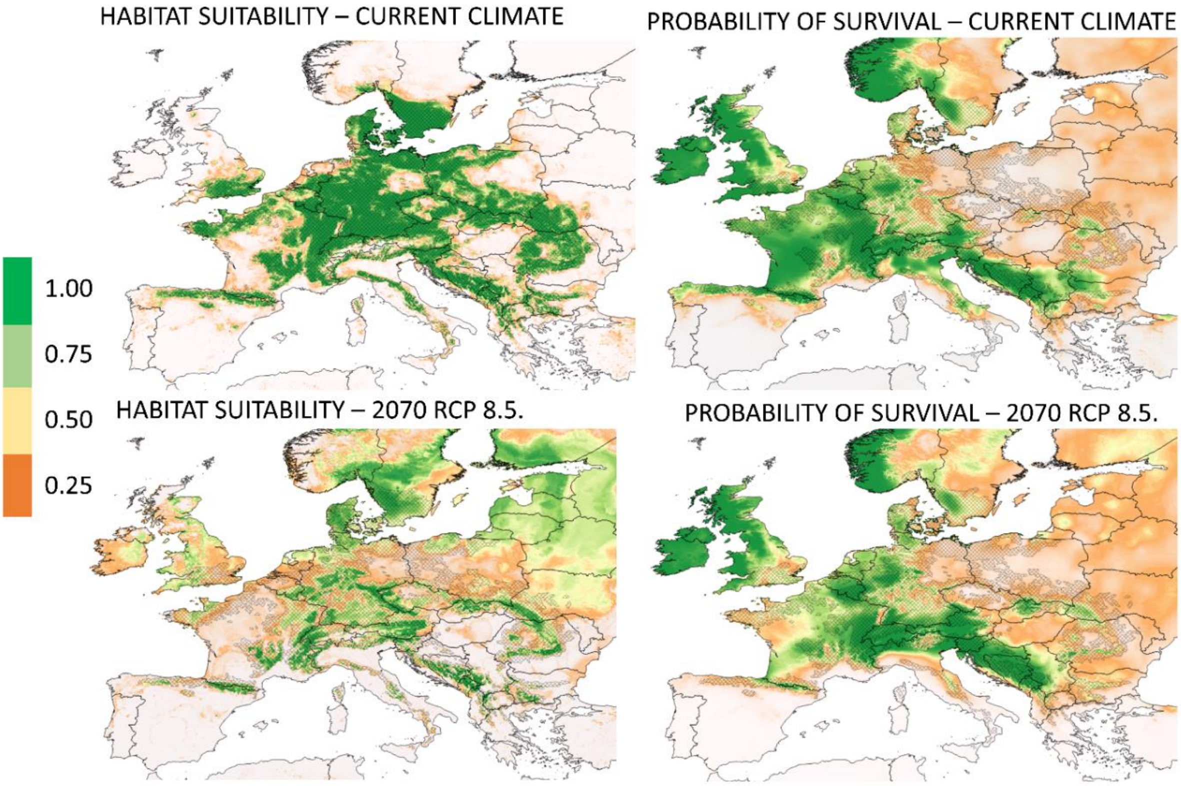


Figure 2. Predictions showing the predictions habitat suitability and probability of survival under current (top) and future conditions (bottom) from a SDM (left) and ΔTraitSDM (right) based on mortality measurements, repectively. Habitat suitability is calculated using the occurrence/absence of the species from Euforgen (http://www.euforgen.org/species/fagus-sylvatica/; showed by dashed envelopes) and by adapting the SDM developed in (Stojnić *et al.*, 2018) to match the same climatic variables as those used by the ΔTraitSDM. Probability of survival is estimated by a ΔTraitSDM based on individual survival of young

trees (adapted from Gárate Escamilla et al. under review) measured in the BeechCOSTe52 network of provenance tests (Robson *et al.*, 2018).

Although undoubtedly important, the contribution of local adaptation to phenotypic trait variation across species ranges is lower than the contribution of plasticity in all the species and traits studied to date (Table 1), suggesting that phenotypic plasticity is generally the predominant component of intraspecific variability. Nevertheless, differences exist in the relative importance of plasticity vs. local adaptation among traits. Overall, height and radial growth show weaker signs of local adaptation to climate than those traits related to phenology (bud burst and flowering) (Duputié *et al.*, 2015; Richardson *et al.*, 2017). As a consequence, the choice of trait used by the ΔTraitSDM conditions the response to climate across the ranges. For instance, ΔTraitSDM based on highly plastic growth-related traits would produce predictions of higher tolerance to climate variation than those based on phenology, which is constrained by local adaptation to current conditions. However, phenology still has a strong plastic component, suggesting that populations can accommodate flowering dates to expected climatic scenarios, as found in *Artemisia tridentata* populations in North America (Richardson *et al.*, 2017).

At an evolutionary scale, phenotypic plasticity could slow down genetic adaptation and hence turn into a counter-productive mechanism for the long-term survival of populations (Oostra *et al.*, 2018). However, over the short-time scale imposed by climate change, having higher plasticity than local adaptation in fitness-related traits is likely to translate into a positive outcome for survival, at least of long-lived organisms like trees that are experiencing significant environmental change within their lifetime. ΔTraitSDM indicate that many tree populations have enough phenotypic plasticity in fitness-related traits to persist *in situ* under commonly used climatic scenarios (Table 1). This is the case for tree growth in *Pinus contorta* (Oney *et al.*, 2013). Similar conclusions can be drawn from ΔTraitSDM based on survival of *Pinus sylvestris* and *Pinus pinaster* considering only the southernmost part of the species' ranges (Benito Garzón *et al.*, 2011). A similar trend in tree-height variation was visible for *Abies alba* across its range, showing that ΔTraitSDM predict a less-restricted distribution than models considering only the occurrence of the species (Pearman *et al.*, 2008; Fréjaville *et al.*, under review).

Quercus petraea and *Fagus sylvatica* are good examples of how plasticity can help populations to persist under climate change. When ΔTraitSDM models of *Q. petraea* are projected into a mild climate change scenario, the survival and growth of populations in its core and northern range show similar patterns to those projections under current conditions. This implies that these populations have high tolerance of changes in climate (Sáenz-Romero *et al.*, 2017; Gárate Escamilla *et al.*, 2019). Comparing a SDM (adapted from Stojnić *et al.*, 2018) and a ΔTraitSDM (adapted from Gárate Escamilla *et al.*, 2019) for *F. sylvatica,* under current (Fréjaville & Benito Garzón, 2018) and future (RCP 8.5. GISS-E2-R) climate scenarios, we can visually inspect some of the differences between both predictions (Figure 2). The SDM is based on the occurrence/absence of the species, whereas the ΔTraitSDM is based on mortality measured across a large network of common gardens (Robson *et al.*, 2018). The large differences visible between SDM and ΔTraitSDM outputs for the present and under future conditions can be interpreted as the result of differences in how each model handles fitness. Whereas *F. sylvatica* SDM is based on a binary assumption of fitness (occurrence/absence), beech ΔTraitSDM is based on a probability of mortality that varies among common gardens and provenances, reflecting different sensitivities of trees to climate as result of evolutionary processes and phenotypic plasticity. Not surprisingly, the SDM prediction perfectly matches the current species distribution range that is the basis of the regression, whereas the ΔTraitSDM prediction gives a lower probability of survival for that part of the range where mortality is high (reflecting low fitness that can have important consequences for the persistence of the species). The divergence between model outputs under future conditions is even higher than those for the present day: ΔTraitSDM indicate very low probabilities of *F. sylvatica* persistence in the East of the range in 2070, whereas SDM do not depict this trend. Another notable difference between model projections, is the larger area where predictions from the ΔTraitSDM suggest *F. sylvatica* will persist from the present to the future (Figure 2), likely resulting from the high plasticity of populations that would help them to persist *in situ*. However, we can expect that considering other traits or combination of traits in ΔTraitSDM would lead to different conclusions, particularly under new climates, where it is difficult to predict trait co-variation and the relationship of traits with climate.

	ΔTraitSDM					**SDM**	**ΔTraitSDM - SDM Comparison**
Species	**TPVE**	**PVEP**	**PVEG**	**Traits**	**References**	**References**	
Abies alba	42			Tree height	(Fréjaville *et al.*, 2019) [1]	(Pearman Peter B. *et al.*, 2008)	SDM show a more restricted distribution than ΔTraitSDM, particularly at the periphery of the distribution.
Artemisia tridentata	79	46	33	Flowering phenology	(Richardson *et al.*, 2017)		
Fagus sylvatica	45 (PVEP+ PVEG) 49 (PVEP + PVEG) 19 (PVEP + PVEG)	- - -	- - -	Tree height D.B.H. Mortality Budburst Fruit ripening Leaf senescence	(Gárate Escamilla *et al. In review*) (Gárate Escamilla *et al. In review*) (Gritti *et al.*, 2013)	(Pearman Peter B. *et al.*, 2008; Gritti *et al.*, 2013; Stojnic *et al.*, 2018)	Differences on the distribution rely on the trait used (ΔTraitSDM). Overall, predictions from ΔTraitSDM show larger potential distribution ranges than those predicted by SDM.
Picea mariana	37	28	9	Tree growth	(Yang *et al.*, 2015)		
Pinus pinaster	43.1 (PVEP + PVEG)	-	-	Tree height Survival	(Benito Garzón *et al.*, 2011)		Reduction in suitable area estimated with SDM by 2080 = 60 %; reduction in suitable area estimated with ΔTraitSDM by 2050 = - 30%
Pinus ponderosa	-	-	-	Tree height	(Rehfeldt *et al.*, 2014)	(Rehfeldt *et al.*, 2014)	Strong differences in tree growth and habitat suitability. No direct comparison of both models done.
Pinus strobus	32	29	3	Tree growth	(Yang *et al.*, 2015)		

Pinus sylvestris	82.4 (PVEP + PVEG) 52.85 (PVEP + PVEG) 33 (PVEP + PVEG)	- - -	- - -	Survival Budburst Survival & radial growth Leaf unfolding	(Benito Garzón *et al.*, 2011; Valladares *et al.*, 2014) (Gritti *et al.*, 2013) (Duputié *et al.*, 2015) (Duputié *et al.*, 2015)	(Benito Garzón *et al.*, 2008a) (Gritti *et al.*, 2013)	Reduction in area estimated with SDM by 2080 = 98%; reduction in suitable area estimated with ΔTraitSDM by 2050 = 1 %
Pseudotsuga menziesii	-	-	-	Tree height	(Chakraborty *et al.*, 2018)	(Chakraborty *et al.*, 2018)	ΔTraitSDM based on growth and SDM show very similar predictions under current climate.
Quercus petraea	60.8 58.1 71 (PVEP + PVEG) 7 (PVEP + PVEG) 24 (PVEP + PVEG)	59.4 56.6 - - -	1.4 1.5 - - -	Tree height Survival Budburst Fruit ripening Leaf senescence	(Sáenz-Romero *et al.*, 2016; Fréjaville *et al.*, 2019) (Duputié *et al.*, 2015)		
Quercus robur	-	-	-	Phenology	(Gritti *et al.*, 2013)[1]	(Gritti *et al.*, 2013)	
Andropogon gerardii	-	-	-	Biomass Height Leaf width Chlorophyll content	(Smith *et al.*, 2017)		

[1] Reaction norms accounting for plasticity are estimated only at the core of the species distribution.

Table 1. Comparison between ΔTraitSDM and SDM outputs for those cases where both types of models exist and local adaptation and phenotypic plasticity have been quantified across species ranges. TPVE: Total percentage of the variance explained by the model; PVEP: Percentage of the variance explained by plasticity; PVEG: Percentage of the variance explained by local adaptation; Traits: phenotypic traits used by the model; References: references from which the data from the ΔTraitSDM and SDM have been extracted for comparison between the two modelling approaches.

2.2.4. Towards multi-trait *ΔTraitSDM*

Although multi-trait approaches are, to date, only conceptually proposed (Laughlin & Messier, 2015; Laughlin, 2018), the flexibility of ΔTraitSDM favours their actual implementation. One possible approach to develop multi-trait ΔTraitSDM is substituting β (equation 1) for a second trait used as a co-variate. For example a model where a co-variate trait (T_2) that affects T_1 across climatic clines can take the form:

$$\beta = b_4 T_2 + b_5 T_2 \times CS + b_6 T_2 \times CP \quad \text{(equation 2)}$$

where T_2 is a trait that co-varies with T_1; b_4, b_5 and b_6 are the coefficients of T_2 and the interactions with climate of the common-garden site (CS) and with the provenance (CP).

Multi-trait ΔTraitSDM draw upon concepts developed in functional ecology that consider weighted-average trait values as a function of species performance to delimit species ranges (Stahl *et al.*, 2014), with the additional strength that they consider intra-specific variation for each of the traits. Trait co-variation can modulate fitness across species ranges (Laughlin & Messier, 2015). Trait co-variation can additionally result in compensatory changes in demographic traits that buffer the negative effects of warming at the trailing edge (Peterson *et al.*, 2018). It can also produce relationships between survival and phenology-related traits that vary across the ranges (Richardson *et al.*, 2017; König *et al.*, 2018), and trade-offs between photoperiod and tree growth that might limit species range expansion at the leading edge (Way & Montgomery, 2015).

2.2.5. *ΔTraitSDM for conservation and management planning*

A direct application of ΔTraitSDM is to help in planning translocation of populations to compensate for climate change (Aitken & Bemmels, 2016; Chakraborty *et al.*, 2016). Translocation of populations within the distribution range is a soft case of assisted migration: an increasingly proposed mitigation strategy for the effects of climate change on species that has generated an intense debate when it implies a change in species composition (Hoegh-Guldberg *et al.*, 2008; Richardson *et al.*, 2009; Hewitt *et al.*, 2011; Pedlar *et al.*, 2012; Schwartz *et al.*, 2012). In contrast, the suggestion of translocation of populations has largely been positively received. Arguments in favour of population translocation are based on population and ecosystem conservation, and the possibility that hybridization provides an evolutionary opportunity for populations to adapt quickly to new climate conditions (Sansilvestri *et al.*, 2015). In the particular case of forest trees, the translocation of populations is mainly based on the rationale that moving populations adapted to warmer climates can help to increase the productivity and/or survival of some marginal populations at the leading edge. Although ΔTraitSDM are a useful tool to evaluate, identify and propose those target populations for translocation, prior to any implementation in the field, the same considerations and trade-offs linked to trait selection for fitness are also important for management purposes: i.e. some populations would have higher growth rates than others, but this does not necessarily imply higher survival or reproductive success. To increases the chances of translocation success, translocation programs need to consider more than one trait in their assessments of populations (Benito-Garzón *et al.*, 2013a).

Ecosystem conservation for the future relies on species vulnerability to climate change: a function of exposure and sensitivity (Williams *et al.*, 2008). Exposure to climate change is estimated from climate change projections and species ranges, for which SDM are an appropriate tool. Species sensitivity refers to species ability to adapt to environmental changes and the physiological tolerance limits of their ecological traits which can be addressed by ΔTraitSDM.

2.2.6. Conclusions, perspectives and limitations of ΔTraitSDM

The ΔTraitSDM approach has been refined over the last decade, producing projected species ranges that are remarkably different from SDM outputs and generally are less alarmist with regard to the consequences of climate change for species in the future. These differences emanate from the inclusion in ΔTraitSDM of plasticity, which can differ among populations across species ranges. The broader scope of ΔTraitSDM calls into question why SDM are still widely used, even for those forest tree species for which common gardens exist. The reason likely reflects technical difficulties in compiling, harmonising and calibrating models using extensive field measurements recorded in common-gardens. However, the continued use of SDM is very unsatisfactory, particularly when these models are presented to supposedly inform and aid costly management decisions such as in conservation and assisted migration programs; our review clearly shows that such decisions should not neglect the capacity of populations to adapt and acclimate to new conditions.

ΔTraitSDM are based on empirical data measured in large networks of common gardens. This is a great strength of ΔTraitSDM but also its main constraint. Although incomplete data can be used in partial analysis, a poor representation of common gardens and provenances can easily compromise the statistical power of ΔTraitSDM that is required to scale-up processes and produce spatial generalisations. This is particularly important in predictive ecology, in which reaction norms inform us about the limits of environmental conditions that populations can withstand. In the context of climate change, one implication of this is straightforward: that new common gardens planted outside the limits of the distribution range of a species are needed to estimate the maximum tolerance of fitness-related traits to new conditions.

To date, ΔTraitSDM have mostly been based on a limited number of traits that are largely related to the survival component of fitness. Although growth and phenology can indirectly impact seed production, therefore affecting fitness through reproduction, direct measurements of reproduction are still missing from ΔTraitSDM. This is mainly because reproduction is largely unexplored at the range-wide scale, and how fecundity and reproduction vary across species ranges is almost unknown (Pearse *et al.*, 2016). In general, we still know little about how well phenotypic traits measured under the experimental conditions of a common garden can represent phenotypic variation and its relation with fitness in natural populations.

Natural selection boosts genetic differentiation among populations but reduces within-population genetic variation by fixing alleles (local adaptation). The potential of populations to adapt to new climates depends on the extent of within-population genetic variation at evolutionarily relevant loci, something that has not yet been addressed by ΔTraitSDM. This variation is however associated with climate across large gradients (Bay *et al.*, 2018). Hence, linking genomics to phenotypic and environmental variation is the natural next step in ΔTraitSDM that will help us explain populations' potential for adaptation under new climate conditions across species ranges.

2.3. Chapter 2. Climate-driven range dynamics of species and biomes

Biomes distribution are changing following climate change and new management strategies. Understanding these changes is challenging because climate is changing at an unprecedented pace. Nevertheless, how biomes reshuffled in the past following climate changes can help us to better understand the novel challenges of biomes and biodiversity. Ecotones are transition zones between two different biomes that can inform us of early warnings of biome shift.

2.3.1. Learning from the past to predict the future

The human signature on the Earth has moved the planet from the Holocene into the Anthropocene (Crutzen, 2002; Corlett, 2014), a new, less climatically stable age with no analogs in the past (Haywood *et al.*, 2011). Rapid climate warming will likely cause extensive changes in the distribution and abundance of species and a concomitant massive reshuffling of local communities (Willis & MacDonald, 2011). Studying relationships between species ranges and climate in the past can help understand new patterns that may emerge under predicted climate change. Envelope models can help identify refugia (i.e., places where species can persist while the surroundings do not any longer sustain them), as shown in the Iberian Peninsula, where models were evaluated against empirical data, showing a good match between model output and paleorecords (Benito Garzón, Sanchez de Dios, & Sainz Ollero, 2008; Calleja et al., 2009). The comparison of the current patterns of the biomes on Earth under global warming using the warmest period of the Holocene (6000 years BP) as a proxy of a future warmer climate can help us to understand the degree of change of climate in the period named as the Anthropocene.

We hypothesize that some biomes will present some climate similarities between the Mid-Holocene and the projected 2100 climate, which would suggest that these biomes can be considered as refugia to climate change because they have already experienced similar temperatures in the past.

To test our hypothesis we compared climate anomalies between the projected 2100 climate and 6000 years BP (Figure 2; (Benito-Garzón, Leadley, & Fernandez-Manjarrés, 2014). However, what we found is that that most of the Earth's biomes will probably undergo changes beyond the mid-Holocene recorded levels of community turnover and range shifts because the magnitude of climate anomalies expected in the future are greater than observed during the mid-

Holocene. A few biomes, like the remnants of North American and Euro-Asian prairies, may experience only slightly greater degrees of climate change in the future as compared with the mid Holocene. The figure illustrates the anomalies (climatic differences) between the expected climate for 2100 and that of the Mid-Holocene. Whereas maximum temperatures are expected to be similar to those of the Mid-Holocene, the maximum temperatures and minimum temperatures are expected to increase by 5 degrees in 2100 in relation with the temperatures recoded in the Mid-Holocene.

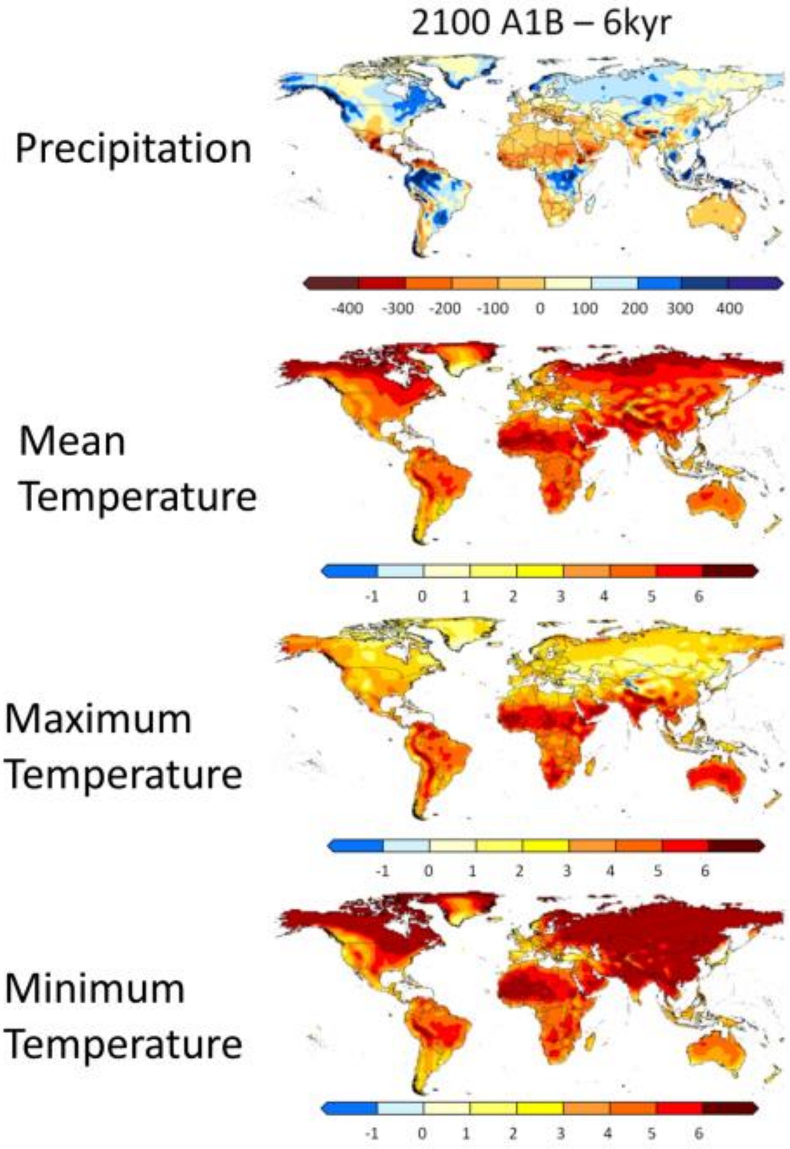
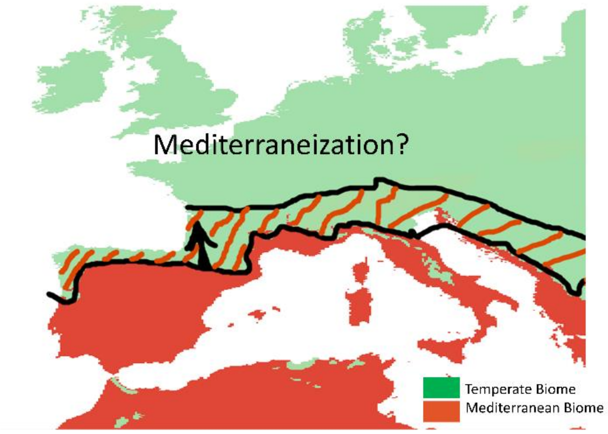


Figure 2. Climatic differences between 2100 (IPCC scenario A1B) and the mid Holocene (6000 years BP): (a) annual precipitation (mm); (b) mean annual temperature; (c) maximum temperature; and (d) minimum temperature. All temperature scales are in °C (figure adapted from (Benito-Garzón et al., 2014)). For precipitation map, blue colors indicate higher precipitation in 2100 in relation with the mid-Holocene and red colors a decrease in precipitation in 2100. For temperature maps, dark red colors indicate an increase in temperatures in 2100 in relation with the mid-Holocene.

The Holocene-Anthropocene climate transition appears to be of greater magnitude from that between the last warm period in the Earth (Mid-Holocene) and the pre-industrial period**.** This implies that many biomes and ecoregions will need to respond to future climate change in ways not observed during the Holocene.

2.3.2. Ecotones may change under climate change: implications

The pace of climate change boosts local extinction of populations at the southern range margin, leaving empty niches for new species. In this context, community ecology and functional biogeography are crucial for better understanding the future of biodiversity (Stahl *et al.*, 2014; Van Bodegom *et al.*, 2014). Community assembly is commonly defined as the process by which species from a regional pool colonize and interact to form local communities (HilleRisLambers *et al.*, 2012), including stochastic and deterministic processes (Lortie *et al.*, 2004). In the context of climate change, one plausible rule for new tree assembly is the *limiting similarity theory*, a trait-based approach in which trait convergence indicates the assemblage of species with similar ecological tolerances (Götzenberger *et al.*, 2012). At a larger geographic scale, functional traits modulate species ranges along environmental gradients (Ackerly & Cornwell, 2007), and they can be used to predict species' geographical limits in relation to current and future climate (Stahl *et al.*, 2014; Van Bodegom *et al.*, 2014). Hence, in the context of climate change, community ecology and functional biogeography would help to identify opportunities for new community assembly along large environmental gradients. Many studies have focused on the likely contraction of Mediterranean species near their southern range edges (Klausmeyer & Shaw, 2009; Underwood *et al.*, 2009; Benito-Garzón *et al.*, 2013d). However, climate change would also offer new opportunities for Mediterranean species to colonize new territories in altitude (Peñuelas & Boada, 2003) and in latitude at the northern edge of their current ranges. For example, *Quercus ilex* has expanded its range northwards in the last decades (Delzon *et al.*, 2013), and other Mediterranean species have the potential to do the same (de Luis *et al.*, 2013). At the same time, many temperate tree species in Western Europe are likely to experience an erosion of their southern range limit edge (Benito-Garzón, Ruiz-Benito, et al., 2013; Urli et al., 2014), leaving empty niches available for other species. Hence, in the ecotone defined between temperate and Mediterranean species (hereafter TME), colonization by Mediterranean species is likely to become a widespread phenomenon. However, to what extent invasive trees would exhibit advantage extrapolated from functional and fitness related traits compared with Mediterranean species has not yet been addressed.



Here we asked the following questions (1) is there already a shift in the ecotone between Mediterranean and Temperate species? Is there a mediterraneization (=increase of Mediterranean species in detrimental of temperate ones) in this ecotone? (2) Which is the role of biological invasion in these ecotones? (3) Which are the socio-economic consequences of changing biomes?

To answer question (1) we look at the local scale in Nouvelle Aquitaine forests. For its position between the temperate and Mediterranean biomes, the Nouvelle Aquitaine region constitute a good gradient to study the evolution of forests at the ecotones over time. We used information on individual tree forests from a three temporal campaigns of the French National Forest Inventory from 1993 to 2014. We used individual growth measurements (diameter at breast height, radial increment, circumference at breast height and basal area) and species occurrence per plot. We showed that Mediterranean and sub-Mediterranean species optimum has shifted from 1993 to 2015 towards higher temperatures (Figure 3). *Quercus suber* showed the highest shift towards warm climates, with almost 1°Celsius; submediterranean species *Q. pyrenaica* and *Q. pubescens* show a slighter shift towards warm climates. However interesting, our findings could be the result of changes in management, and a longer time frame should be used to confirm that mediterraneization is taken place in the Nouvelle-Aquitaine region.

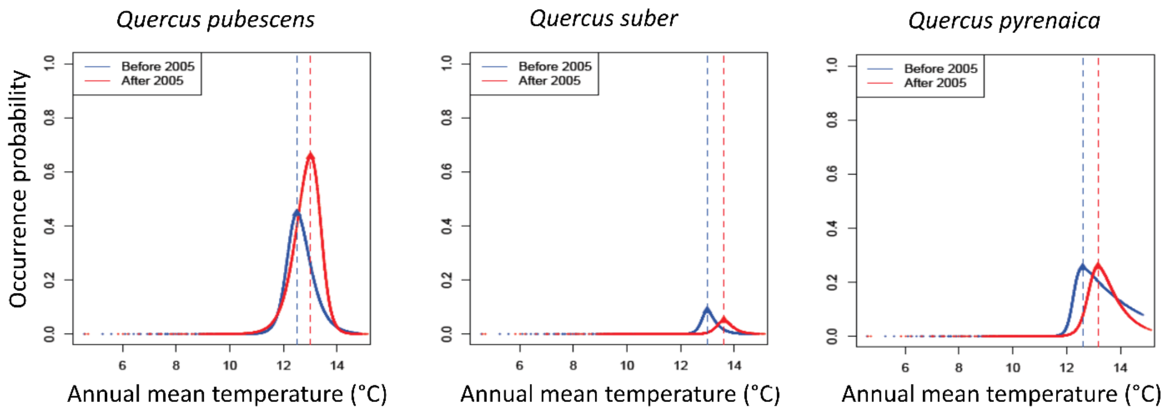


Figure 3. Probability of species occurrence as a function of the annual mean temperature found in plots from the NFI grouped before (blue lines) and after (red lines) 2005. Dotted lines indicated the optimum temperature for the species (adapted from Boudou-Aguirre Master 2 Thesis, University of Toulouse, 2017)

To answer question (2) we delimit the habitat suitability of American invasive trees in Europe under climate change scenarios. Invasive alien species are also part of the local pool along the TME, and whether they may colonize empty niches and experience significant increases in abundance needs to be investigated. We studied invasion processes by alien tree species in the TME in the light of the *empty niche hypothesis* (Stachowicz & Tilman, 2005) that focuses on the invasibility of habitats and poses that the availability of empty niches are the major driver of the success of invasive species.

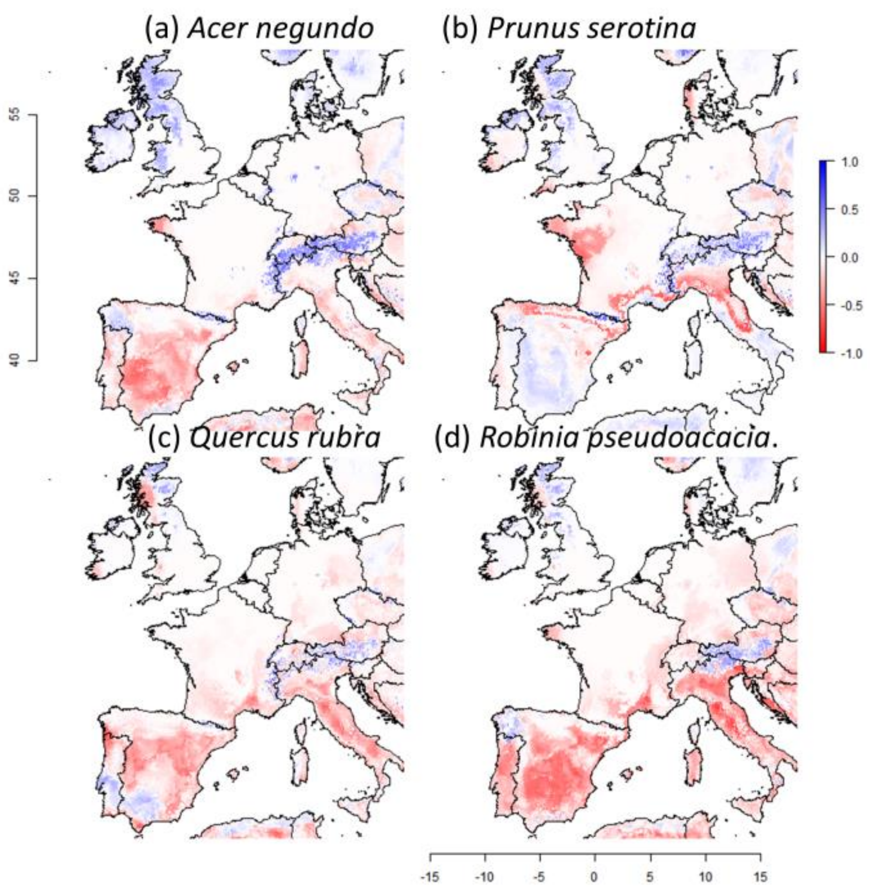
Climate change and biological invasions are considered the most important causes of biodiversity loss after natural habitat destruction (Corvalan *et al.*, 2005). A strong effect of modern rapid climate change on the abundance and impact of biological invasions is expected in the near future (*e.g.*, (Sutherst, 2000; Hellmann *et al.*, 2008; Walther *et al.*, 2009; IPCC, 2014). Because new climates will generate ecological opportunities (i.e., empty ecological niches), invasive species peaks are predicted for the future. Yet, some authors agree on an overall decrease of invasive species habitat suitability under future climate change as predicted by SDM but with a very high interspecific variability (*e.g.*, (Peterson *et al.*, 2008; Bellard *et al.*, 2013).

We built species distribution models calibrated with occurrence data from the main North American invasive trees in Europe (*Acer negundo*, *Prunus serotina*, *Quercus rubra* and *Robinia pseudoacacia*) and projected them over Europe and North America (Figure 4).

First results indicate that all four species have experienced a real shift of their climatic niche from their native (North America) to their invasive (Europe) ranges. Our results also suggest that the invasion potential of the four species under climate change will be highest in central and northern Europe (Climate scenario: RCP - 4.5) (Camenen *et al.*, 2016), and not in the TME, however the consequences of our modeling approach in the ecotone between temperate and boreal biomes need to be explored. Further analysis are need on the ground of the *evolutionary imbalance hypothesis* (Fridley & Sax, 2014), that focuses on the invasiveness of species and assumes that fitness differences are its most important driver. Recent works show that some functional traits related to fitness likely promote invasiveness (van Kleunen *et al.*, 2010; Heberling & Fridley, 2013).

Figure 4. Habitat suitability (HS) calculated for four invasive species. Models were calibrated from presence and pseudoabsence data from North America and Europe. Habitat suitability ranges from 0 (= not suitable) to 1 (highly suitable). Results are shown in differences in HS as predicted for models by 2050 (RCP 4.5) in relation with present conditions.

🟦 Increase of HS
⬜ No changes in HS
🟥 Decrease of HS



To answer question (3) we reviewed the literature regarding the socio-ecological systems in the savanna-Mediterranean and Mediterranean-temperate ecotone ecosystems. We identify a few ecotones in Western Europe (Figure 5).

One of the main conclusions extracted from our review is the increase of hardwood (oak-like) trees in detrimental of gymnosperms in the ecotones in Western Europe, together with a progression of scrubland a grassland grounded on the increase of drought in the region. In the worse-case scenario, a spread of non-productive scrubs along the ecotone would irreversible transform the current vegetation to a less productive one.

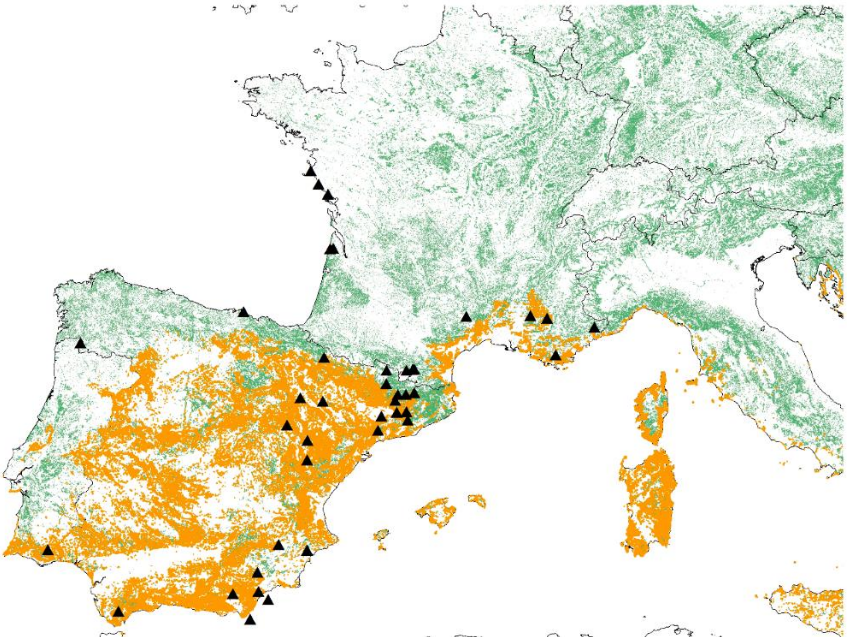


Figure 5 Current observations of increasing evergreen tree density in the study area in South-Western Europe (black triangles). Most records show the expansion of the holm oak (*Quercus ilex*), but other species such as *Quercus pubescens* and *Juniperus* spp. have also been recorded. The brown color represents sclerophyllous and transitional vegetation, and the green color forests including green broadleaved and conifer forests from the CORINE Land Cover 2012 (from (Fernández-Manjarrés *et al.*, 2018)).

2.3.3. Related publications

Fernández-Manjarrés JF, Ruiz-Benito P, Zavala MA, Camarero JJ, Pulido F, Proença V, Navarro L, Sansilvestri R, Granda E, Marqués L, Temunovič M, Bertelsmeier C, Drobinski P, Roturier S, **Benito-Garzón M**, García de Cortazar-Atauri I, Simon L, Dupas S, Levrel H, Sautier M (2018). Forest Adaptation to Climate Change along Steep Ecological Gradients: The Case of the Mediterranean-Temperate Transition in South-Western Europe. *Sustainability*, *10*(9), 3065.

Camenen, E., Porté, A. J., & **Benito Garzón, M.** (2016). American trees shift their niches when invading Western Europe: evaluating invasion risks in a changing climate. *Ecology and Evolution*, *6*(20)

Benito Garzón M, Leadley, P W & Fernandez-Manjarrés J F (2014). Assessing global biome exposure to climate change through the Holocene - Anthropocene transition. *Global Ecology and Biogeography*, *23*, 235–244.

Benito Garzón M, Sanchez de Dios, R., & Sainz Ollero, H. (2008). The evolution of the Pinus sylvestris L. area in the Iberian Peninsula from the last glacial maximum to 2100 under climate change. *The Holocene*, *18*(5), 705–714.

Benito Garzón M, Sanchez de Dios, R., & Sainz Ollero, H. (2008). The evolution of the Pinus sylvestris L. area in the Iberian Peninsula from the last glacial maximum to 2100 under climate change. *The Holocene*, *18*(5), 705–714.

Benito Garzón M, Sánchez de Dios, R., Sáinz Ollero, H. (2007). Predictive modelling of tree species distributions on the Iberian Peninsula during the Last Glacial Maximum and Mid-Holocene. *Ecography*, *30*, 120-134

2.4. Chapter 3. Traits and processes at species ranges

2.4.1. Delimiting species ranges with phenotypic trait variation

The potential distributions of species under future climates have been extensively explored by means of modeling techniques generally known as species distribution models (SDM), a potentially powerful tool for generating hypotheses about suitable habitats for species under new climates and restoration options (Dawson *et al.*, 2011). However, these SDM can produce very biased predictions of species suitability when they are only based on species presence or absence (Hampe, 2004). Some recently emerged approaches (reviewed in Chapter 1) to improve the realism and specificity of SDM rely on the use of fitness or survival data either from natural populations (typically growth rates quantified in forest inventories) or from field tests in provenance trials (Wang *et al.*, 2010; Benito Garzón *et al.*, 2011; O'Neill & Nigh, 2011; Benito-Garzón *et al.*, 2013d; Oney *et al.*, 2013; Benito-Garzón & Fernandez-Manjarrés, 2015; Vizcaíno-Palomar *et al.*, 2017). The links between climate, biotic factors across contrasted environments, fitness and species ranges is still unexplored. For example, tree demography would be determinant in defining species range limits. In addition to demographic traits and their likely importance for the global fitness, the study of the intra-specific variation of the traits can help us to understand how populations, rather than species, would adapt and acclimate to new climates, and which traits and processes would be determinant for doing so. Here I explain some of the main results that we obtained in the last years on the role of tree mortality to define the southernmost part of the species ranges, the importance of phenotypic plasticity versus local adaptation for demographic traits across species ranges, and some applications to forest managements under new climates.

2.4.2. Tree mortality

Tree mortality is a key process that determines forest structure, community assembly (Loehle, 1998) and, at a larger scale, the ranges of the species (Purves, 2009; Benito-Garzón *et al.*, 2013d) in natural ecosystems. However, the multifactorial nature of tree mortality makes difficult to understand its spatial patterns (Lines *et al.*, 2010; Ruiz-Benito *et al.*, 2013). In general, at the leading edge of the distributions, mortality is mainly leading by frost (Morin *et al.*, 2008) whereas at the rear edge of the distributions mortality is driven by the complex interaction between tree size, competition, and drought (Brodribb & Hill, 1999; Lines *et al.*, 2010; Benito-Garzón *et al.*, 2013d; Ruiz-Benito *et al.*, 2013). In addition, the long history of management is clearly shaping the ranges of the species, the structure of the forests and tree growth (Gómez-Aparicio *et al.*, 2011).

If water stress periods are much longer in the future, as expected by the IPCC climate scenarios for most of the Mediterranean area, plant water potential can drop and provoke air embolisms that block xylem vessels and reduce the ability of the trees to move water from soils to the leaves (Tyree, 1999). However, trees vary dramatically in their tolerance to drought induced embolism making predictions of how forests might be altered more difficult. The difference between the minimum water potential measured in the plants under natural conditions (φ_{min}) and the water potential at which 50% loss of the conductivity occurs (φ_{50}) represents the hydraulic safety margin (Choat *et al.*, 2012). Although it is known that most forest species in the world currently operate with narrow hydraulic safety margins against potentially deadly levels of drought stress (Choat et al. 2012), the geographical variation of the hydraulic safety margin in the current and future climate change conditions still remains unknown, specially within the distribution range of the species.

We ask the following questions: (1) which are the main drivers (including climatic, specific drought tolerance of the species, forest structure and competition) of tree mortality in Western Europe and how they interact in a geographical cline? (2) How is tree mortality related to the interspecific resistant to drought or to the increase in pathogens affecting trees?

To tackle the first question we develop individual tree models of mortality based on the recorded mortality calculated from 6 National Forest Inventories from Spain to Finland (Figure 6).

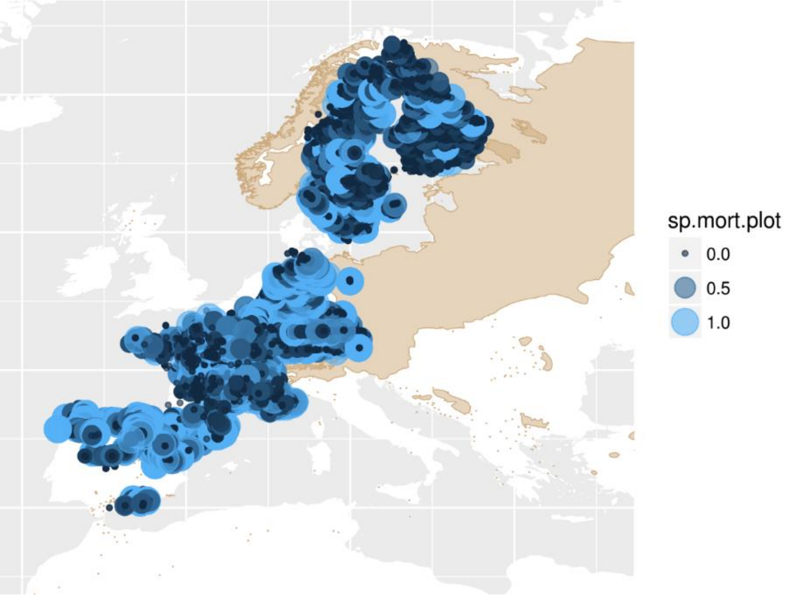


Figure 6. Mortality rates per plot of *Pinus sylvestris* in Europe (data source: FunDiv Europe + French NFI).

In the particular case of *Pinus sylsvestris* and *Fagus sylvatica*, competition and drought were the two main drivers of mortality, with significant interactions between them across species ranges (Figure 7). The relative importance of drought related variables and competition on Scots pine mortality was constant across biomes, with higher relative importance of competition over drought related variables all across the range (Figure 7). Both intra-specific and inter-specific competition were detrimental for Scots pine survival, showing the species' low competitive capacity. On the contrary, our results analyzing beech mortality point out drought as the main driver of beech mortality all the range (Archambeau et al. submitted). This is explained by the high capacity of beech to outcompete to our species, and hence is less sensitive to inter-specific competition.

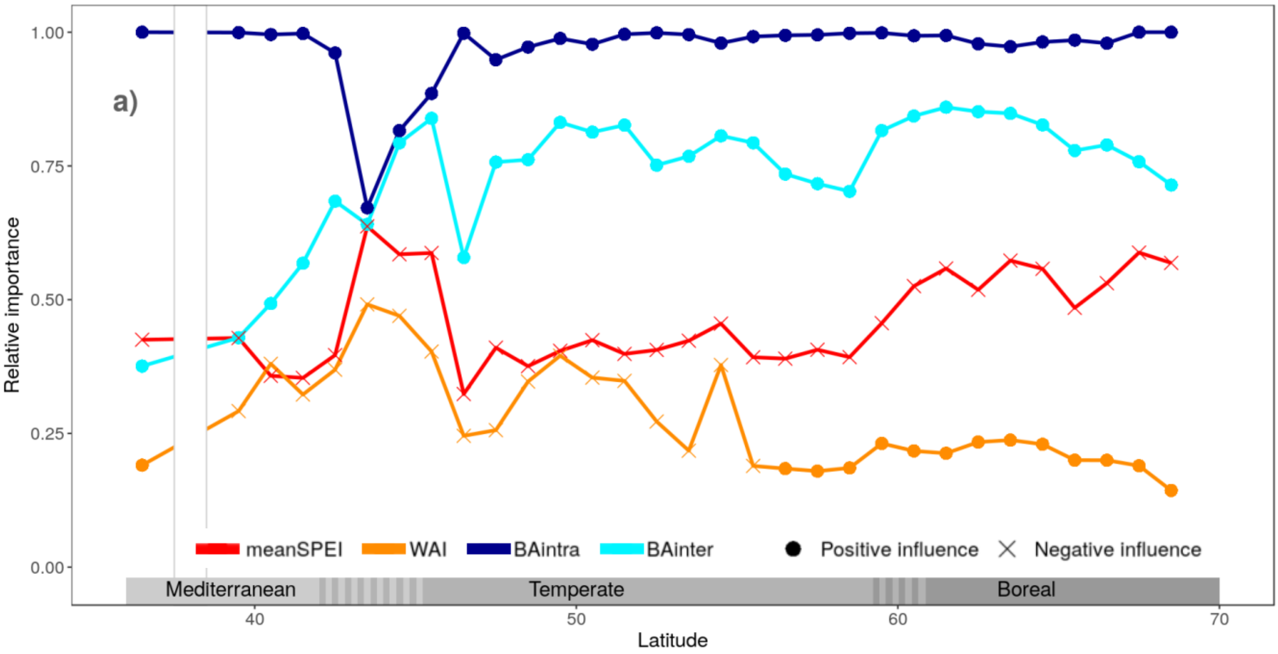


Figure 7. Relative importance of drought (i.e. *meanSPEI* & *WAI*) and competition (i.e. *BAintra* & *BAinter*) for Scots pine probability of mortality. The relative importance was computed for each tree from the logistic regression model. The relative importance of the most influencing variable had a value of one and the relative importance of other variables was scaled accordingly. For each variable, the relative importance's values were aggregated by 1° latitude resolution and the points of the graph correspond to the average values. The white section corresponds to missing data (due to *P. sylvestris* distribution in Spain: abundant in the northern mountains and then jumping to the Nevada range in the south). (From Archambeau *et al.* submitted.)

To tackle the second question we analyzed the legacy of water deficit by comparing observed mortality in populations having experienced negative and positive hydraulic safety margins, in particular at the drier edge of species ranges. To achieve our aim, we combined in hurdle models spatial information of modelled soil water potential from climate data and soil texture maps with average mortality from 193,261 plots belonging to 44 species recorded in the French and

Spanish National Forest Inventories (NFIs) with the species' threshold of hydraulic failure measured in laboratory conditions (W50/88). We were able to identify those populations of each species that have operated with a negative hydraulic safety margin over the last 30 years and the relative effect of the modelled hydraulic safety margin in average mortality. Although each species show a different patter, for some of them as shown for the case of *Larix decidua* in the Figure 8, populations show a significant interaction effect between the aridity conditions and the effect of being operating with negative or positive safety margin. This interaction was different in most of the species, for example in *Larix decidua* those populations having operated with negative hydraulic safety margin are those showing higher mortality, and mortality was always higher in those populations inhabiting more arid conditions.

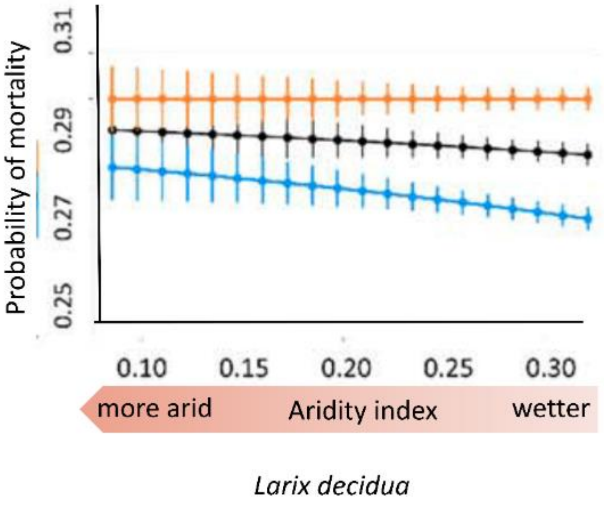


Figure 8. Mortality of *Larix decidua* predicted across an aridity gradient at the rear edge of its distribution (aridity index = mean annual precipitation/mean annual potential evapotranspiration). Populations occurring with negative hydraulic safety margin (orange line), populations occurring with positive hydraulic safety margin (blue line) and populations occurring at average hydraulic safety margin (black) are shown. Mortality decreases towards wetter climates and populations with negative hydraulic safety margin show always higher mortality than the others (from Benito Garzón et al. 2018).

2.4.3. Processes: Local adaptation and phenotypic plasticity at wide-range scale

Understanding forest adaptation to climate change relies on the knowledge of the main mechanisms that allow sessile organisms to survive under changing climates: genetic adaptation and phenotypic plasticity. Phenotypic plasticity and local adaptation are the most important processes that would allow some populations to persist under new climates. Nevertheless, species distribution models have rarely included these process in their predictions. Whereas traditional niche models consider that all populations of a given species are identical, the reality is that local adaptation and plasticity can strongly modulate the relationship of populations with climate as shown by ΔTraitSDM. To quantify these mechanisms we need tree plantations where the origin of the seed sources is well known (i.e. provenance tests, common gardens, genetic trials). The most important shortcoming of ΔTraitSDM is usually the quality of the data from common garden that are difficult to compile, harmonise and analyse. We have compiled many provenance test that are now freely available in public repositories for some species: *Abies alba* (Benito-Garzón *et al.*, 2018), *Fagus sylvatica* (Robson, Benito Garzón, & BeechCOSTe52 database consortium, 2018); Figure 9), *Pinus pinea*, *Pinus nigra* and *Pinus pinaster* (Koskela *et al.*, 2013) .

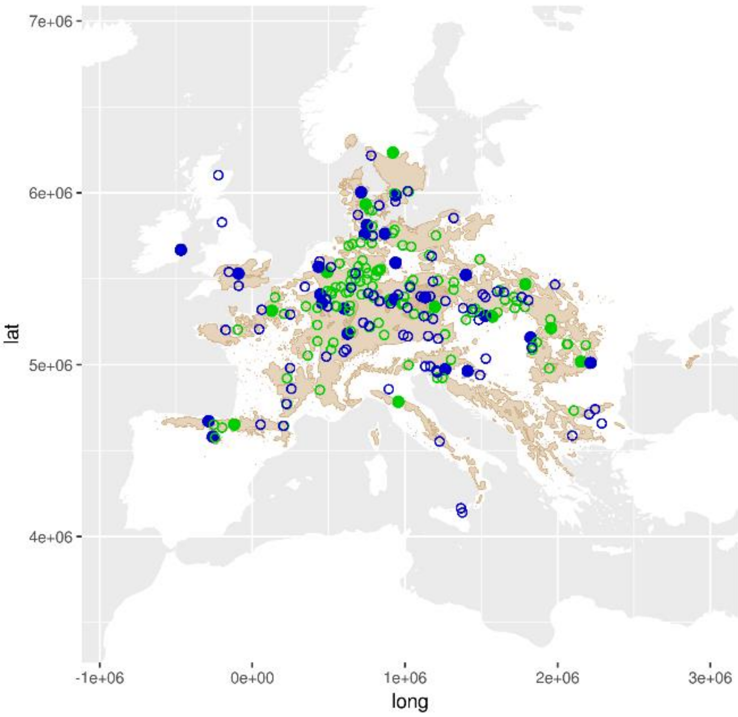


Figure 9. Example of provenance test network for the case of *Fagus sylvatica*. Location of the genetic trials established in 1995 (green solid circles) and 1998 (blue solid circles) and the respectively provenances tested in 1995 (green empty circles) and 1998 (blue empty circles) series. Only locations and provenances for which phenotypic traits have been measured are represented. The distribution of *Fagus sylvatica* from Euforgen (http://www.euforgen.org/species/fagus-sylvatica/) is reproduced in light brown. (Robson *et al.*, 2018)

These extensive data base compilations from European species across their distribution ranges has grounded our research in understanding the role of phenotypic plasticity and local adaptation and its geographical variation; in particular we have tackled the following questions:

(1) Can we compare the predictions of SDM with those of ΔTraitSDM directly? Which are the limitations and main strengths of forecasting species range shifts accounting for phenotypic plasticity and local adaptation?

(2) Are there feasible alternatives to common gardens to estimate local adaptation and phenotypic plasticity at wide-range?

To **answer question (1)** we explicitly compared the output of an SDM based on the occurrence of *Pinus sylvestis* and *Pinus pinaster* in Spain with that of a ΔTraitSDM calibrated with individual tree survival as a proxy of fitness recorded in a network of provenance tests.

SDM show overall a more pessimistic output than ΔTraitSDM (Figure 10), suggesting that the capacity to acclimate and adapt to new climates needs to be considered to understand the future of species ranges (Benito Garzón et al., 2011). Figure 10 and Figure 2 illustrate these differences between classical niche models and ΔTraitSDM based on the survival of populations across the ranges.

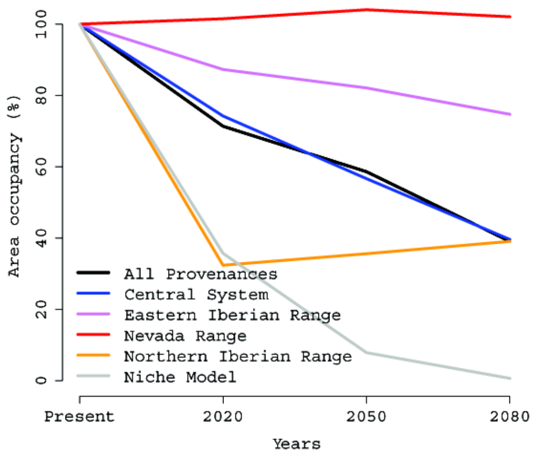


Figure 10. Percentage of the suitable area estimated for *Pinus sylvestris* under the present conditions, and three future climatic periods: 2020, 2050 and 2080 (scenario A2, IPCC). The percentage of habitat suitability is considered as 100% for the present conditions. Results from traditional niche models based on the occurrence of the species is shown in grey (grey; data from (Benito Garzón, Sánchez de Dios, & Sainz Ollero, 2008)), and predictions of models by provenance region calibrated on the survival data measured in provenance trials is shown in yellow (Northern Iberian range provenance), blue (Central System provenance), violet (Eastern Iberian range), red (Nevada range) and black (all the provenances together). Figure modified from (Benito Garzón et al., 2011)).

In a broader context, we examined how intraspecific variation in thermal niches and phenotypic plasticity will affect species distributions in a warming climate (Valladares *et al.*, 2014). We developed a conceptual model that links reaction norm, niche breadth and species ranges for different populations of a virtual species inhabiting a climatic gradient in Europe. We simulated populations' fitness in a framework of different but equally likely scenarios of plasticity and local adaptation: (1) no differentiation among populations, (2) local adaptation and equal plasticity of all populations, (3) local adaptation and high margin plasticity, (4) local adaptation and high central plasticity and (5) and high leading edge plasticity. Here I show the result for warm marginal populations (local adaptation and high margin plasticity scenario) in comparison with that expected from a SDM (no differentiation among populations). The species projections under new climates suggests that high plasticity in warm marginal populations would increase the possibilities to survive of these populations under warmer scenarios (Figure 11).

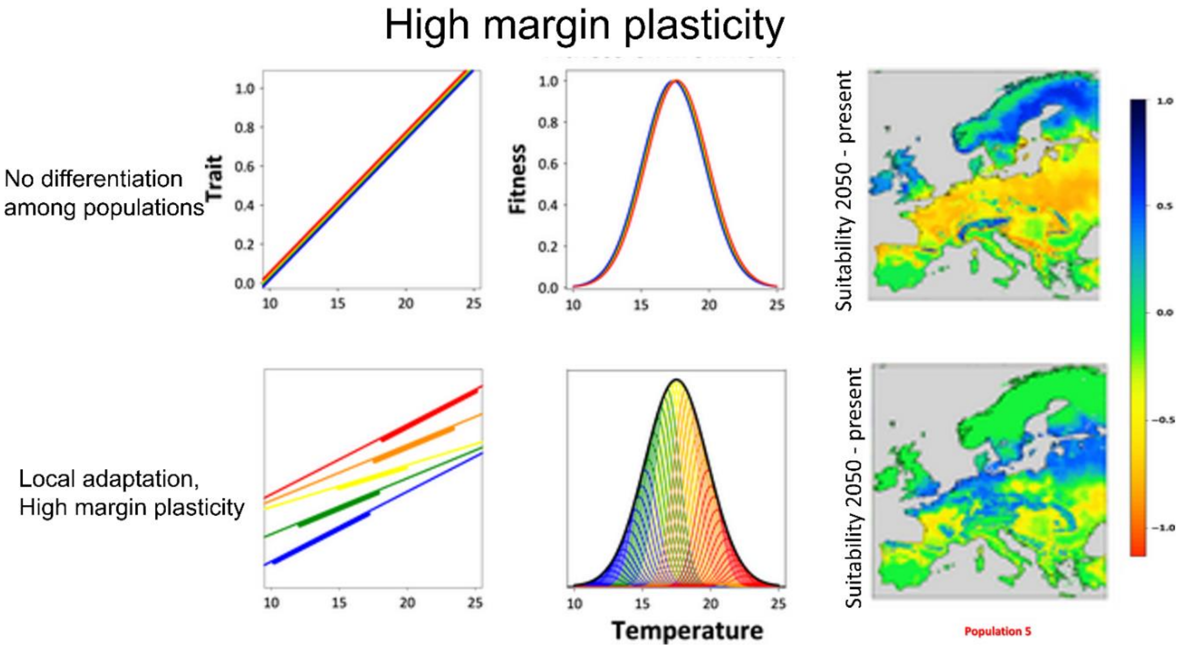


Figure 11. Conceptual model of trait values and fitness vs. environment (temperature) for a virtual species for a populations with high margin plasticity scenarios. Left: Reaction norms of a fitness-related trait in response to temperature for five populations (consisting of different subpopulations) in two different scenarios of intraspecific variation. Trait values are presented in a 0 to 1 arbitrary scale. Thicker sections of each reaction norm represent the section of the environmental gradient corresponding to the range of temperatures experienced by each population. Middle: Fitness-environment curves for each population; each curve represents the fundamental niche for each population. Fitness is presented in a 0 to 1 arbitrary scale. Reaction norm graphs are for illustrative purposes only; the depicted relationships between reaction norms and the corresponding fitness-environment curves are not based on mathematical equations. Right: differences in habitat suitability estimated from 2050 to present projections estimated from the fitness-environment curves for the cases of equal plasticity among populations (top) and high margin plasticity (bottom); for the latter case only the warm populations (red) is projected in the map (adapted from Valladares et al. 2014).

We concluded that including phenotypic variation in ecological models strongly changes the predictions for future species ranges and that available databases (including functional traits intraspecific variation) need to be compiled across large environmental clines to inform such models.

To answer question 2 we estimated the relative variation of tree height with a model that can be calibrated with common garden or National Forest Inventory (NFI) data. In either case, tree height variation is related to the short-term climate (plasticity) and long-term climate of the provenance of the trees (local adaptation) making the assumption that trees from National Forest Inventories have a local origin. This modeling framework (Figure 12) allow us to test

NFI as an alternative network to common gardens data that are usually difficult to compile and harmonize.

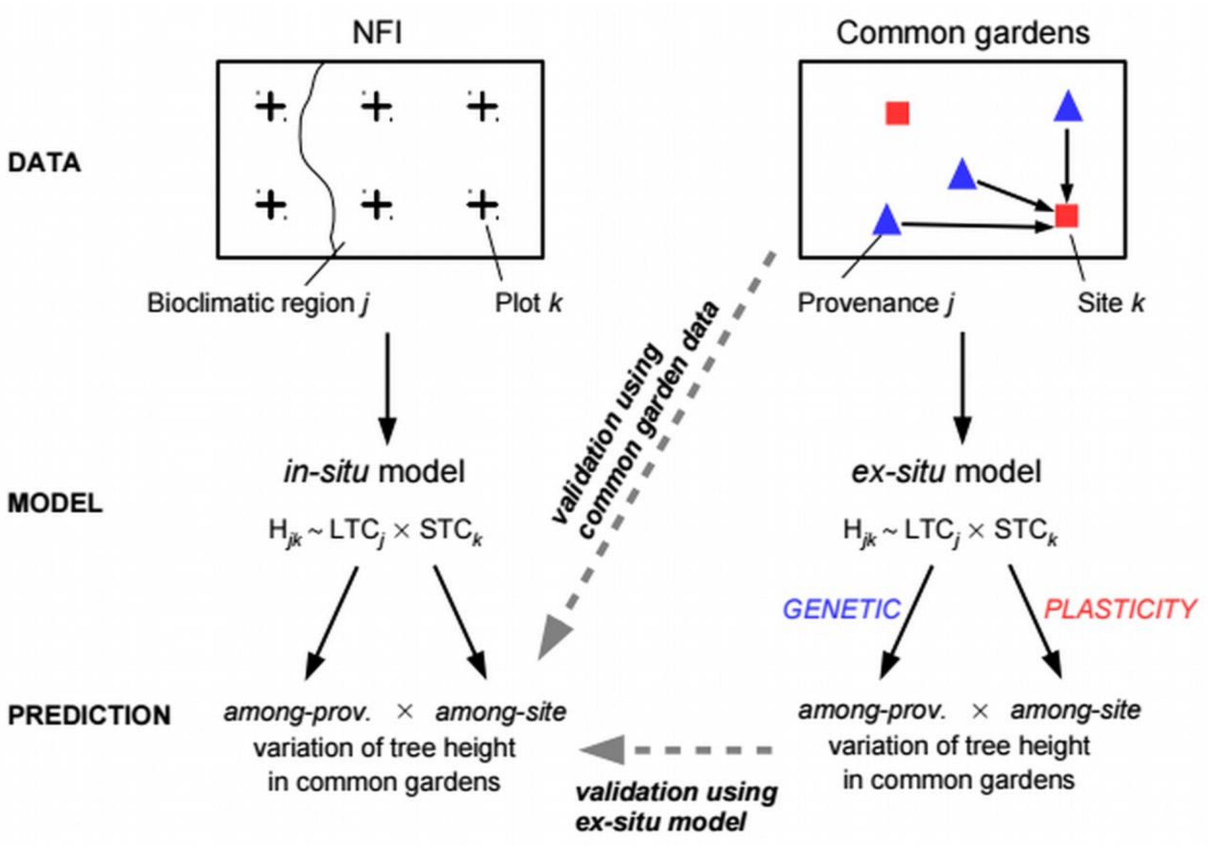


Figure 12. Modeling approach based on a calibration of a mixed-effect model using in-situ observations from NFI to disentangle genetic effect, plasticity and their interaction on intraspecific trait variation (grey square). We used two alternative methods: (1) validation using model (ex-situ and in-situ) comparison; and (2) validation using common garden data (from Fréjaville *et al.* In review)

We test our hypothesis for the particular case of *Abies alba* and *Quercus petraea*. For the latter, the model calibrated with common garden or with NFI data showed similar spatial patterns, and they were both able to accurately separate the relative variation of tree height for genetic, plasticity and their interaction effects. These results open a new perspective on the use of field observations at wide range as those coming from NFI to decompose range-wide intraspecific variation into its genetic, plastic and their interaction components (Figure 13)

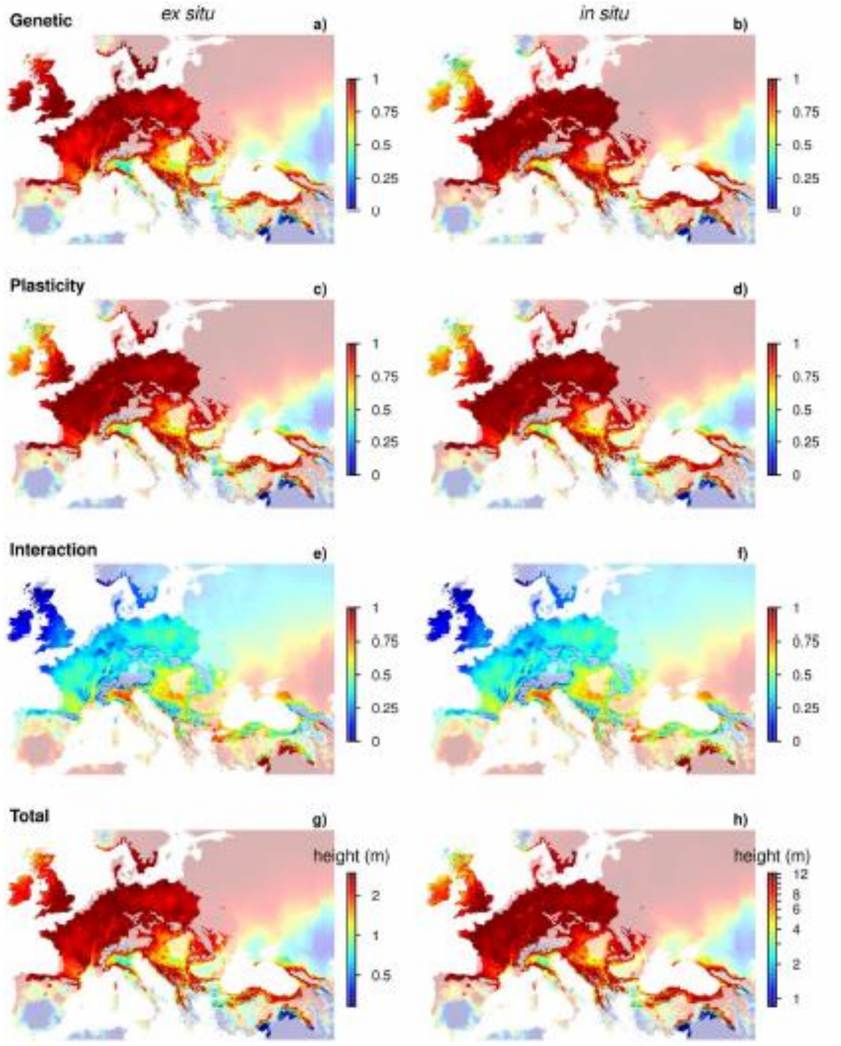


Figure 13. Spatial predictions of genetic, plasticity and their interaction of Quercus petraea height variation using common garden (ex-situ) and NFI (in-situ) data to calibrate the model (Fréjaville et al. In review).

2.4.4. Related publications

Archambeau J, Ruiz-Benito P, Ratcliffe S, Fréjaville T., Changenet A, & **Benito Garzón M**. Determining the role of climate and competition on background mortality of *Pinus sylvestris* L. and *Fagus sylvatica* L. along the European latitudinal gradient using National Forest Inventories. (In review)

Gárate Escamilla H, Hampe A, Vizcaíno Palomar N, Robson TM & **Benito Garzón M**. Range-wide variation in local adaptation and phenotypic plasticity of various fitness-related traits in *Fagus sylvatica* (In review)

Vizcaíno-Palomar N, **Benito Garzón M,** Fady B. Geographic variation of tree height of three pine species (*Pinus nigra* Arn., *P. pinaster* Aiton and *P. pinea* L.) gathered from common gardens in Europe and North-Africa (In review)

Fréjaville T, Fady B, Kremer A, Ducosso A, **Benito Garzón, M**. Inferring phenotypic plasticity and local adaptation to climate across tree species ranges using forest inventory data (In review)

Robson T.M.*, **Benito Garzón M.***, BeechCOSTe52 Database Consortium. (2018) Phenotypic trait variation measured on European genetic trials of *Fagus sylvatica* L. *Scientific Data* 5: 180149. **Joint first author contribution.*

Wan Q., Zheng Z., **Benito Garzón, M.**, Petit R.J. (2018) Interspecific niche stability but intraspecific niche differentiation in *Platycarya*: are ecological niche models relevant for studying niche evolution? *Journal of Plant Ecology*

Benito Garzón, M.*, González Muñoz N.*, Fernández-Manjarrés, J. F., Wigneron J.P., Moisy C., Delzon S. (2018) The legacy of water deficit on populations having experienced negative hydraulic safety margin. *Global Ecology and Biogeography* 27: 346-356. **Joint first author contribution.*

Vizcaíno-Palomar, N., Ibáñez, I., **Benito-Garzón, M**., González-Martínez, S. C., Zavala, M. A., Alía (2017). Climate and population origin shape pine tree height-diameter allometry. *New Forests, 48* (3), 363-379.

Valladares, F., Matesanz, S., Araujo, M. B., Balaguer, L., **Benito Garzón, M.**, Cornwell, W., Gianoli, E., Guilhaumon, F., van Kleunen, M., Naya, D. E., Nicotra, A. B., Poorter, H., Zavala, M. A. (2014). The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. *Ecology Letters, 17,* 1351-1364.

Benito Garzón, M., Ruiz-Benito, P., Zavala, M. A. (2013). Inter-specific differences in tree growth and mortality responses to environmental drivers determine potential species distribution limits in Iberian forest. *Global Ecology and Biogeography*, *22*, 1141-1151

Benito Garzón, M., Alia, R., Robson, T. M., Zavala, M. A. (2011). Intraspecific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography*, *20*, 766-778.

2.5. Chapter 4. Management and adaptation of forests to climate change.

An increased synergy of scientists and stakeholders is needed to adapt forests to a changing climate; this involves making innovative decisions in a context of high uncertainty. Adaptation options for managed forests include for instance changing rotation times, incorporating lesser used local species into harvesting, managing forest structure to diminish fire risks and competition for water among others (Millar *et al.*, 2007; Hoegh-Guldberg *et al.*, 2008). One increasingly considered option for adapting forests to rapid climate change is the translocation of biological material (Hoegh-Guldberg *et al.*, 2008; Richardson *et al.*, 2009; Schwartz *et al.*, 2012). Translocations of tree populations have been done for centuries (Benito-Garzón *et al.*, 2013d), yet the recently proposed concept of assisted migration (AM) proposes for the first time to translocate biological material in order to compensate for future climate change (Richardson *et al.*, 2009). This particular management option has generated an intense debate in the last years, particularly in North America (Hoegh-Guldberg *et al.*, 2008; Richardson *et al.*, 2009; Hewitt *et al.*, 2011; Pedlar *et al.*, 2012; Schwartz *et al.*, 2012). Arguments in favor of AM rely on species and ecosystem conservation whereas arguments against AM are mainly related with the risk of invasion by the focal species and the social acceptance of changing species (Hewitt *et al.*, 2011). In Europe, where no AM program exists yet, the situation is very different from that of North America where many forests are used for wood production and publicly managed. In fact, the debate on the feasibility of AM in European forests is only starting now (Benito-Garzón et al., 2013; Benito-Garzón & Fernandez-Manjarrés, 2015; Benito-Garzón, Ha-Duong, Frascaria-Lacoste, & Fernandez-Manjarrés, 2013; Isaac-Renton, Roberts, Hamann, & Spiecker, 2014). However, different AM options would lead to different climate-related risks and need to be considered separately (see Figure 14).

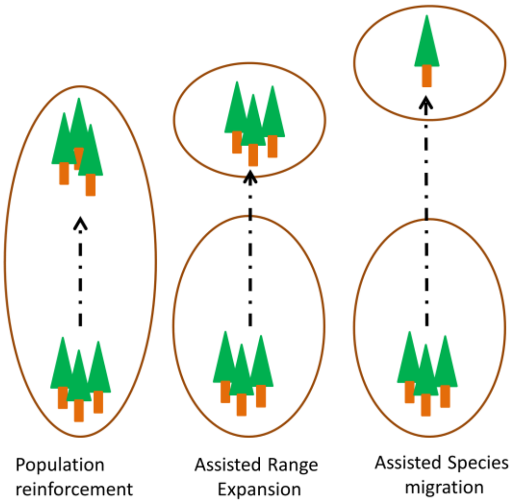


Figure 14. Assisted Migration types including population translocation within the range of the species (population reinforcement), within the historical range of the species (assisted range expansion) and introduction to new species outside the historical and current range of the species (assisted species migration). Figure adapted from (Williams & Dumroese, 2013).

I have focused on the particular case of population reinforcement also known as population translocation or assisted gene flow (Aitken & Bemmels, 2016), which is a managing solution that also happened in the past. To evaluate population translocation for the main species in Europe before any field implementation we asked the following questions:

1) Are there any experiments of population translocation in the past? Did they succeed or fail? Which were the main problems that occurred?
2) Can we test all the likely scenarios of AM *in silico* with the current databases before implementing them in the field? Which are the main challenge that we would find to design AM scenarios?

To **answer question 1** we illustrated the case of the failure of *Pinus pinaster* population translocations in the past (Figure 15). Translocation of populations from Portugal to the Landes in south-western France occurred after great fires in 1950 in the Landes region which contributed to the neglect of the local seed bank. The strong frost event that occurred in the Landes in 1985 was followed by an increase in the mortality of the Iberian populations, whereas the local populations were far less affected, showing the importance of local adaptation of populations. In Aquitaine, climatic variability is characterized by strong peaks of frost with a 10 – 20 years of time lag. In 1986 temperatures reached -22°C in the region. On the contrary, the lowest temperature recorded in the last century in Leiria was only -7.8 in 1941. This brings our attention to the importance of considering climatic variability and particularly extreme events before implementing translocations in the field.

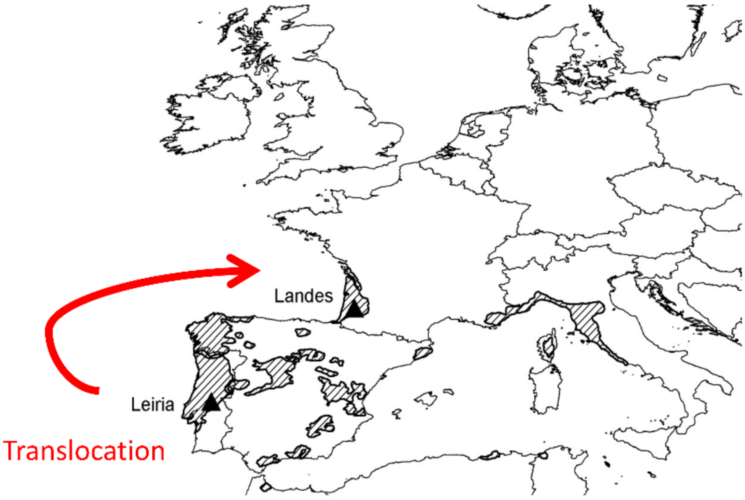


Figure 15. Location of the populations translocated from Leiria (Portugal) to the Landes (France). Dashed area shows the natural distribution range of *Pinus pinaster* in Europe (from (Benito-Garzón *et al.*, 2013b))

To **answer question 2** we generated likely scenarios of population translocation for different species (*Pinus halepensis*, *Pinus pinaster* and *Abies alba*), based on different traits linked to fitness (tree height and survival) and different databases (common gardens and NFI). Using a combination of volume accumulated and mortality, our models showed that volume and mortality trends are not always correlated with seed sources and target zones (Figure 16).

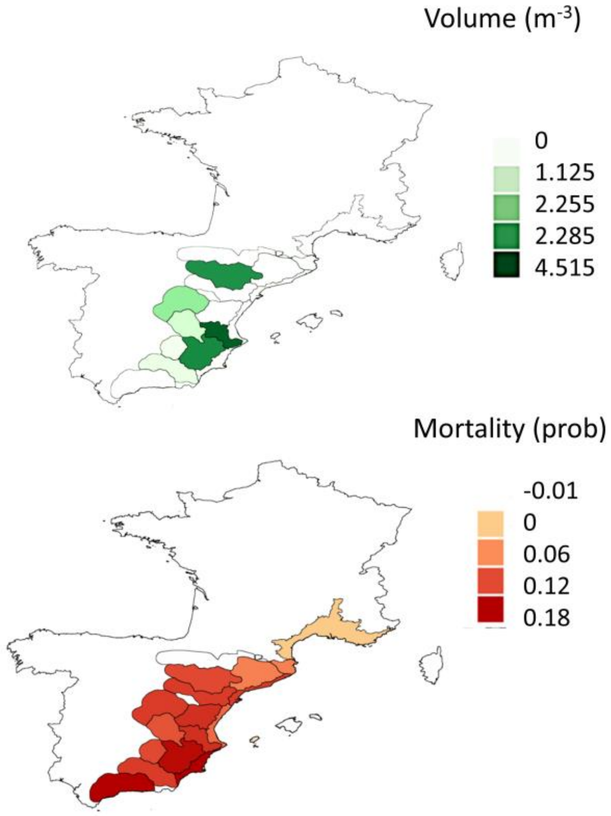


Figure 16. Projected differences in volume and mortality of *Pinus halepensis* between present climate and the IPPC A1B climate scenario for 2050. Models were calibrated with the volume and mortality recorded in French and Spanish National Forest Inventories and projected for the entire territory. The final maps are averaged by provenance region. The maps show that volume and mortality do not show similar geographical patterns. For example, mortality is higher in the Southern part of the range than in the North, whereas the volume is higher in the core of the range (from (Benito-Garzón & Fernandez-Manjarrés, 2015)).

This results highlight the lack of decision tools in forest management, particularly to select target zones and seeds for translocations adapted to future conditions. We explored the consequences of using decision theory to implement assisted migration for the case of *Abies alba* populations as measured in the French provenance trials (Figure 17), with the cautionary conclusion that there is not best decision to reduce uncertainty at the long term (Benito-Garzón *et al.*, 2018).

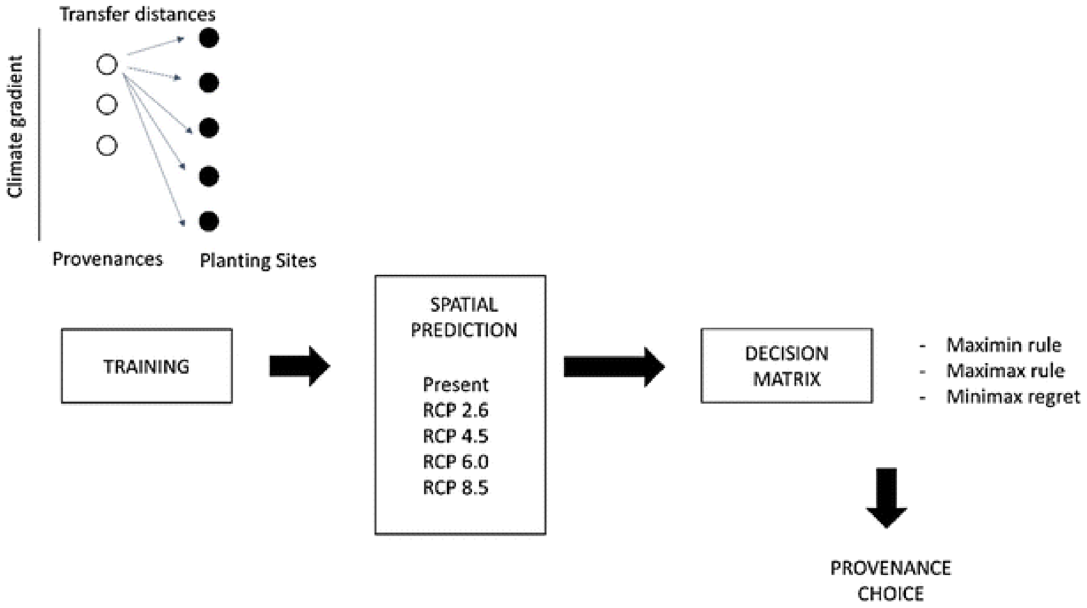


Figure 17. Flow diagram depicting the main steps for decision-making under uncertainty for selecting the preferable translocation option. Climatic transfer distances between the origin of the provenances and the planting sites where the trees are growing are used to train a non-parametric model of tree height. Then, spatial predictions are performed for each of the target zones (in this case, the same locations where the planting sites were established). These predictions by target zones are compiled in a decision matrix that allows us to apply standard decision rules to select preferable options for translocation (from (Benito-Garzón et al., 2018)).

2.5.1. Related publications

Benito Garzón, M., Fady B., Davi H, Vizcaino-Palomar N., Fernández-Manjarrés, J. F. (2018) Trees on the move: Using decision theory to compensate for climate change in forest social-ecological systems. *Regional Environmental Change* 18: 1427-1437.

Benito Garzón, M., Fernández-Manjarrés, J. F. (2015). Testing scenarios for Assisted Migration of Forest Trees in Europe. *New Forests, 46*, 979-994.

Benito Garzón, M., Ha-Duong, M., Frascaria-Lacoste, N., Fernández-Manjarrés, J. F. (2013). Extreme climate variability should be considered in forestry-assisted migration. *Bioscience, 63*, 317.

Benito Garzón, M., Ha-Duong, M., Frascaria-Lacoste, N., Fernández-Manjarrés, J. F. (2013). Habitat restoration and climate change: dealing with climate variability, incomplete data and management decisions with tree translocations. *Restoration Ecology, 21*, 30-36.

3. PERSPECTIVES

Some of the research topics that I highlight in this section are projects at their early stage (including submitted projects), but others are at an earlier step, only ideas for the future that try to cover those points in which I would make a contribution to current knowledge on scaling up processes in biogeography. In either case, they constitute the next step of my scientific career, and they ground on my previous research experience.

3.1. Towards a multi-species multi-trait variation approach for understanding species ranges and their responses to ongoing climate change

3.1.1. Getting information from new and old provenance tests networks

It is our responsibility to take care of the precious information contained in provenance test data cumulated over years to understand how tree populations can cope with changes in climate. I will continue collecting and harmonizing data from old provenance test across Europe to understand the role of fitness-related traits and their co-variation at wide-range scale to delimit species ranges under a changing climate and to provide new management tools to face forest vulnerability under new climates.

Although doubtless interesting, old provenance tests present several problems, (i) they have not generally been designed to understand the effects of climate change across the range and hence have been established in few sites that generally do not cover all the species ranges (but see exceptions as the one of European beech - Figure 9), (ii) information is difficult to gather because of different policies across countries and (iii) data measured inside is usually difficult to harmonize because they are the issue of several plantations over time, with different protocols followed.

To overcome most of these problems, a new network of provenance tests across Western Europe has been established by the European Forest Institute: REINFFORCE (Resource infrastructures for monitoring, adapting and protecting European Atlantic Forests under changing climate; EFI Atlantics; Figure 18). The provenance tests of the REINFFORCE network covers all the European Atlantic Coast for many tree species, including temperate, Mediterranean and exotic trees. This provenance tests network encompasses 38 plantation along a steep latitudinal gradient from Azores Islands to Scotland. 35 native and non-native species from at least 3 different origins have been planted in every common garden. Trees were planted in 2010, and phenotypic traits will be measured during 15 years since the plantation. To this end, a common protocol has been applied to monitor tree growth (height growth), health status (and mortality), and phenology (bud burst and leaf falling).

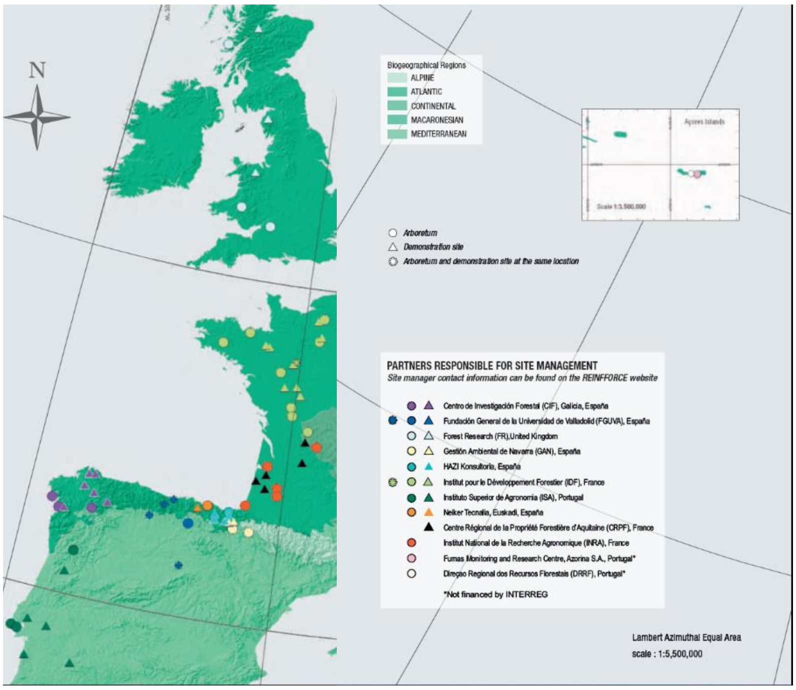


Figure 18. REINFFORCE network of provenance tests. Circle and triangles forms show slightly different experiments called arboretum and demonstration sites, respectively.

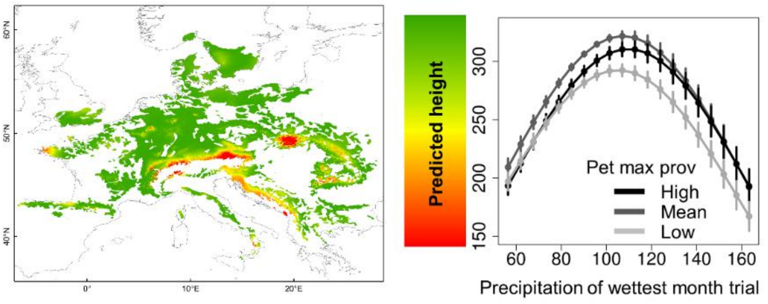
In a first step we will compare fitness-related traits models (ΔTraitSDM) for those species and traits shared between old European trials and the REINFFORCE network. Old provenance tests have an experimental design where trees coming from many origins (usually covering the entire species distribution range) are planted in a few common gardens (usually planted in the core or leading part of the species distribution range), whilst REINFFORCE network have only three different origin of trees (from the core, lead- and rear-edge of the species distribution ranges) but planted in 38 common gardens covering the entire distribution ranges and often plantations are established outside the current species ranges. This contrasted experiments can be used to understand the minimum number of trials need to quantify the ecophysiological limits of the species (phenotypic plasticity);

3.1.2. Trait co-variation at wide-range species distribution ranges

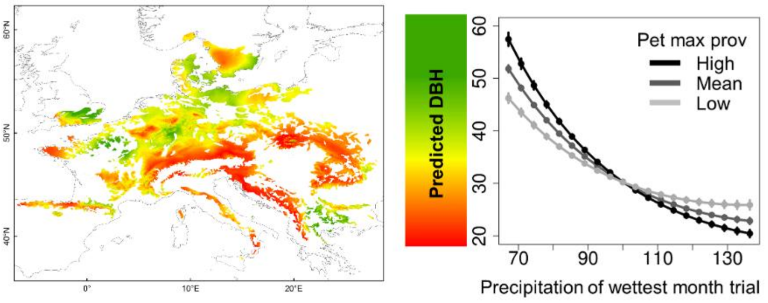
Improving species distribution models goes through the understanding of fitness at geographical scales, as discussed in Chapter 1. However, fitness depend on the co-variation of several traits (Laughlin & Messier, 2015; Laughlin, 2018). Those traits directly related to fitness as for example growth and phenology and eventually survival, show remarkable differences at wide-range scales (Figure 19). Phenotypic variation on functional and extended phenotypic traits is less well known, even if they can affect fitness over species ranges. To date, we know that populations differ in their sensitivity to drought across its range, possibly owing to the plasticity of xylem embolism resistance of this species (Wortemann *et al.*, 2011; Benito Garzón *et al.*, 2018b; Stojnic *et al.*, 2018), and the plasticity of functional and physiological traits of leaves and photosynthesis (Drake *et al.*, 2017; Patterson *et al.*, 2018). Physiological traits associated with stomatal responses tend to exhibit higher plasticity than the corresponding morphological traits, which rely on the production of new organs (Mclean *et al.*, 2014). In addition to direct effect on plants, increasing temperatures are also expected to have detrimental effects on the size and phylogenetic diversity of leaf microbial communities, which are known to vary greatly along climatic gradients (Cordier *et al.*, 2012; Vacher *et al.*, 2016a).

My long-term perspectives include the understanding of how functional and extended phenotypic traits geographical variation can shape species ranges with the further implications under new climates. Although plants are generally adapted to local conditions, the extent to which this adaptation is partially driven by microorganisms as part of their extended phenotype is poorly understood (Lankau & Keymer, 2018). The contribution of above- and below-communities of associated microorganism to tree fitness is also unknown, but it seems that under certain conditions of stress as for example nutrient limitation (Haas *et al.*, 2018) or drought (Pausas & Verdú, 2010; Vacher *et al.*, 2016b), microorganisms can improve trees' fitness. Within the total spectrum of microorganisms associate to trees, we can expect that those specialists differ in their contribution to the total fitness from those generalists over a given tree species range (Merges *et al.*, 2018). More generally, climate change is known to affect the below- and above-ground communities of microorganisms associated with trees, that are part of their extended phenotype (Whitham *et al.*, 2008) and controlled by trees' genotype and abiotic environment (Crutsinger, 2016).

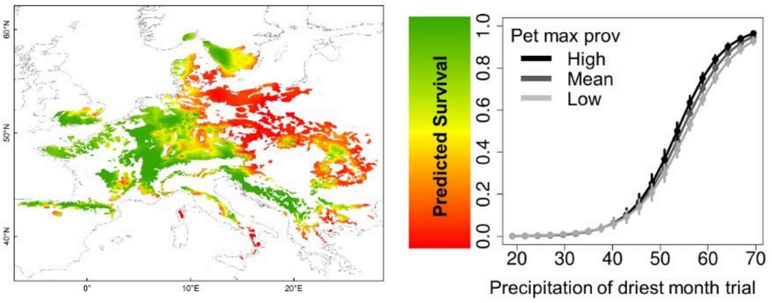
(a) Height



(b) DBH



(c) Survival



(d) Leaf flushing

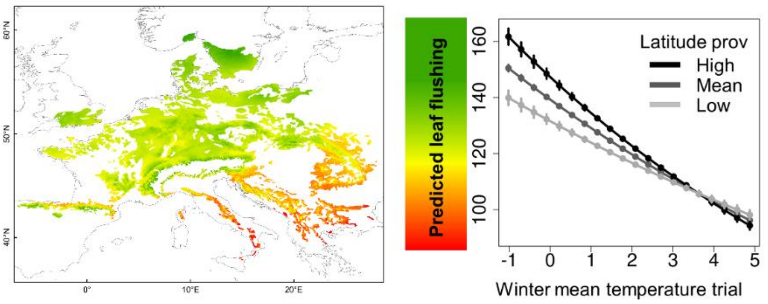


Figure 19. Spatial predictions (maps) and significant interactions graphics (inset) generated using one-trait models of (a) tree height, (b) DBH, (c) survival and (d) leaf flushing of beech models generated with the Robson et al. 2018 database. Colors black, grey, and light grey represent high, medium and low values of the climatic variable for which the interaction is shown. In the inset showing the interaction the (a) y-axis indicates the predicted height in centimeters and the x-axis represent the precipitation of the wettest month of the trial, interacting with the maximum evapotranspiration of the provenance; (b) y-axis indicates the predicted DBH in millimeters and the x-axis represent the precipitation of the wettest month of the trial, interacting with the maximum evapotranspiration of the provenance; (c) y-axis indicates the predicted survival rate and the x-axis represent the precipitation of the driest month of the trial, interacting with the maximum evapotranspiration of the provenance; (d) y-axis indicates the leaf flushing in days and the x-axis represent the winter temperature of the trial, interacting with the winter temperature of the provenance. The maps display the prediction of for contemporary climate (2000-2014) across the species range. The color gradient depicts the clinal variation from lower (red) to high (green) values of the traits (From Gárate Escamilla et al. in review).

Main collaborators: Christophe Orazio (European Forest Institute – EFI Atlantic), Arndt Hampe (BIOGECO), Corinne Vacher (BIOGECO) and Nicolas Fanin (EPHYSE).

Students and Postdocs associated: Homero Garate Escamilla (PhD 2017- 2020); Natalia Vizcaino Palomar (post doc 2016-2020); Marie Curie Postdoctoral fellowship submitted by Asier Herrero.

Funding: GENTREE and B4EST (H2020). ANR JCJC under construction.

3.2. Are there common patterns of wide-range adaptation and plasticity of forest tress to climate in Europe? If so, which are the main drivers of local adaptation and phenotypic plasticity across species ranges?

Plants rely on local adaptation and phenotypic plasticity to cope with climate change (Mclean *et al.*, 2014; Valladares *et al.*, 2014; Roches *et al.*, 2018). Plasticity implies a rapid response to environmental changes and hence likely positive response to ongoing climate change (Mclean *et al.*, 2014; Reich *et al.*, 2016), whilst local adaptation is the result of a long term response that can constrain populations capacity to survive under new climates (Frank *et al.*, 2017) by adaptation lags to current climate (Pedlar & McKenney, 2017). Although both processes are ubiquitous in plants they are still unexplored at a wide-range scale.

Phenotypic plasticity allows a tree phenotype to adjust across environments by changes in physiology, morphology or development (Nicotra *et al.*, 2010a; Valladares *et al.*, 2014). Multiple evidences suggest that higher environmental variation at spatial and/or temporal variation come together with higher trait plasticity. These results can be framed within the climatic variability hypothesis (CVH; (Janzen, 1967)). CVH suggests that latitudinal variation in climate should shape the evolution of broader physiological tolerances ranges and, in turn, should determine topographic resistance to dispersal and, through this, influence geographic range size. Likewise, we hypothesize that temporal variation can shape the evolution of physiological tolerances over years, producing more plastic phenotypes in those locations where high environmental variation occurred in the last century.

The most conspicuous results of local adaptation across species ranges is the existence of different climatic optimums (i.e. the climatic conditions that maximize phenotypes) among populations grounded on the centre-periphery theory that stems from the idea that gene flow limits local adaptation in peripheral populations. At the wide-range scale, abundant gene flow from the core of the species range towards marginal populations could induce mal-adaptation in the latter (Rehfeldt *et al.*, 1999). Being maladapted at the leading (cold) margin and the rear (warm) margin can have very different implications under a climate that is warming up: it can be positive for populations at the leading-edge that receive alleles adapted to warmer climates of the core of the distribution range whereas it can be negative for populations at the rear-edge that would have an increase of maladaptation if gene flow from core populations is adapted to cooler climates (Davis & Shaw, 2001; Aitken *et al.*, 2008; Kremer *et al.*, 2012). According to the centre-periphery hypothesis, we expect that climatic core populations would be locally adapted to their climate of origin, whereas we expect that cold and warm margin populations would likely be ‘maladapted’ with positive lags regarding the direction of climate change for cold populations and negative lags regarding the direction of climate change for warm populations.

The compilation of provenance tests that we have done for more than 5 years is now giving us access to enough data on intraspecific trait variation for several species to understand how adaptation and plasticity patterns are distributed in trees at a wide-range scale. We are currently starting to analyze together all these phenotypic data from several species to understand how species and traits are being adapted to climate: are temperature or precipitation the main drivers for natural selection? Are there geographical common patterns of adaptation or phenotypic plasticity for forest trees? If there are geographical patterns of phenotypic plasticity and genetic adaptation to climate, which are the implications under new climates?; why some populations are more plastic that others?; Which are the main drivers of phenotypic plasticity?

Using models as those described previously, based on tree height variation across several major tree species ranges, we will quantify the plastic and genetic component of most of *Pinus pinaster*, *Pinus pinea*, *Pinus nigra*, *Abies alba*, *Quercus petraea*, and *Fagus sylvatica* at the core, cold and warm ranges of the species.

To test whether there is some dependence of phenotypic plasticity on the differences on climate variation across populations covering all the species ranges, we derived plasticity indexes from our models of trait variation for each provenance and related it with the variation in maximum temperature that occurred in each of the provenance during the last century. The preliminary results show that in general, those populations showing higher plasticity are those that have suffered high variability in temperature during the last century (Figure 20), suggesting that climate variability favors adaptation towards plastic genotypes.

We could continue analyzing at a global scale patterns of phenotypic variation using old and new provenance tests as those managed by Reinfforce.

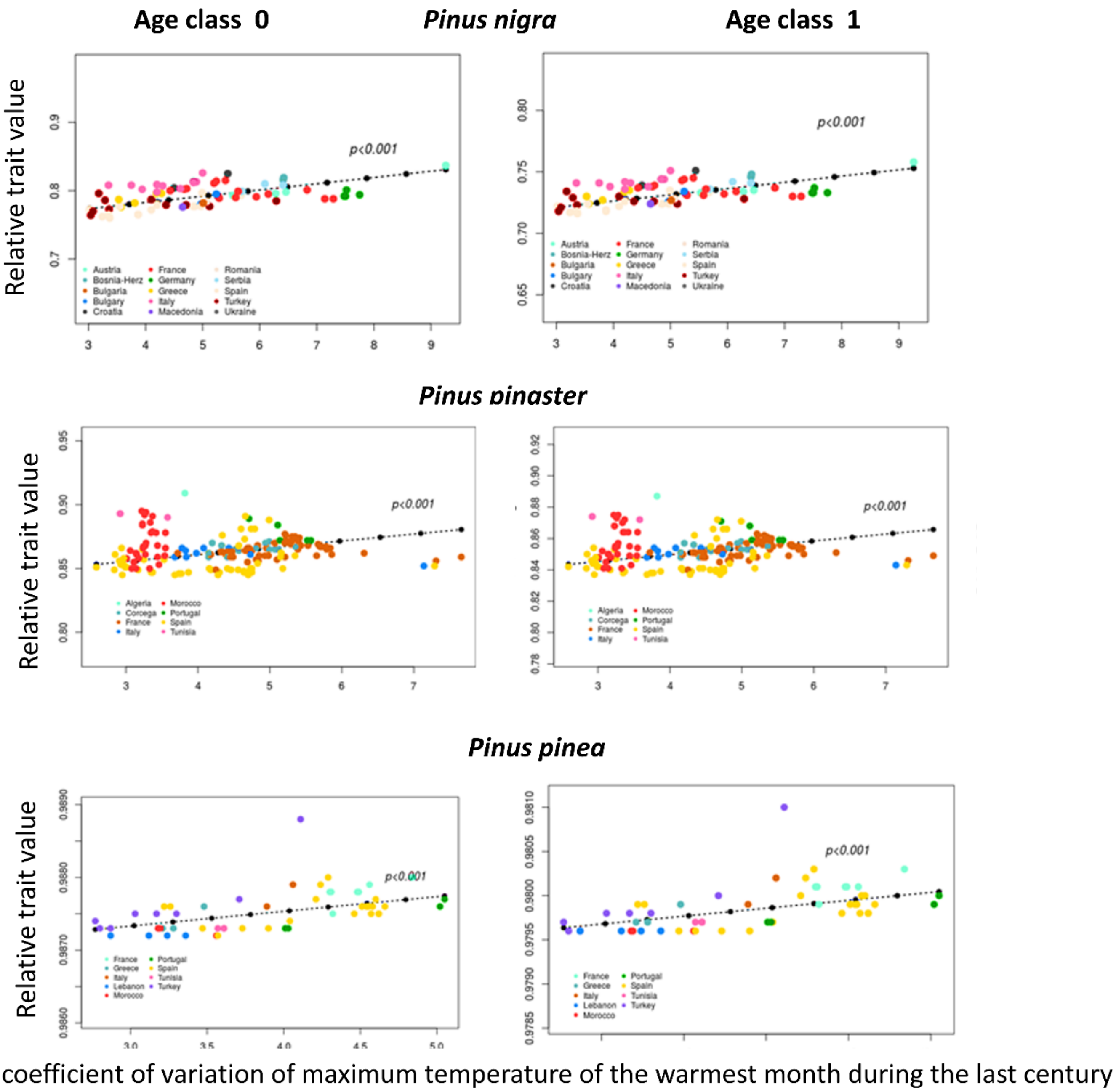


Figure 20. Linear regression between phenotypic plasticity of tree height values across populations of *Pinus nigra*, *P. pinaster* and *P. pinea* and the coefficient of variation of maximum temperature of the warmest month in those populations in the last century. $R^2 = 0.62$. (From Vizcaino Palomar et al. in review)

Postdocs associated: Thibaut Fréjaville (2016-2019) & Natalia Vizcaino Palomar (2016-2020). Marie Curie fellowship in preparation with Asier Herrero.

3.3. Monitoring tree reproduction across species ranges.

Among all the traits potentially linked to tree fitness, it is difficult to figure out which traits would be more important for species to survive under new climates, particularly because species ranges will likely rely on different traits at the leading, core and rear part of their distribution (Hampe & Petit, 2005; Lafontaine *et al.*, 2018). This implies that trait contribution to overall fitness varies across species ranges, with further implications for emerging ΔTraitSDM that are overall, based on single traits, mainly tree growth, survival and phenology. Seed production, quality and phenology are all directly linked to tree fitness (i.e., the contribution of an individual or a population to the next generation). Accordingly, climate drivers tend to increase seed production in northern populations (Övergaard *et al.*, 2007; Drobyshev *et al.*, 2010), and cause a decline in seedling density in southern ones (Barbeta *et al.*, 2011). However, reproduction, a key component of tree fitness and forest regeneration, remains largely unexplored, mainly because it is logistically difficult to assess in the field. The fruiting phenology is largely unknown because its monitoring needs multiple visits across the season. Generally, seed production is measured using seed traps installed at the beginning of the fruiting season and removed at the end of the season. This methodology provides data on the quantity and quality (mass) of seeds of a given population but does not allow further exploration of fruiting phenology and its relationship with climate (Pearse *et al.*, 2016), which would likely modulate the onset of the fruiting season and therefore the success of germination and the expansion or contraction of species ranges (Jackson *et al.*, 2009).

To fill this gap, I developed an electronic device for the automated measurement of tree reproduction at wide-range scale. It was originally developed to measure beechnuts as they drop in beech common garden. This electronic system is based on a network of micro-controllers connected to a funnel beam installed in each seed-fall trap that automatically count falling seeds. The devices save information on daily seed-fall on SD (Secure Digital) cards and send this information by GSM (Global System Communications) technologies to our webserver (http://147.210.209.109). Sensors for humidity and temperature have been added to micro-controllers to allow us to obtain daily weather data of the common gardens.

Figure 21. On the left, first electronic seed trap device installed in Little Wittenham, Oxfordshire, England. On the top, beechnut proving early reproduction on 25 years old beech tree in Little Wittenham trial. August 2018.

The first field campaign held in August 2018, with 5 electronic disposals installed in the 'Little Wittenham' beech common garden in England, where beeches have already started to show early reproduction (Figure 21). The experiment will be repeated in the coming years in England and in other provenance tests in Europe, namely in France and Sweden, two of the beech trials for which thinning is expected in 2018/2019, which would likely promote masting as it happened in the English trial. The long term perspective is to use this procedure to establish an international network for monitoring fruiting across species' distribution ranges.

Main collaborators: Andrea Bertoldi (Institute d'Optique Aquitaine), T. Matthew Robson (University of Helsinki), Régis Burlett (BIOGECO).

Funding: *SeedBeech* (2018-2019); ANR JCJC under construction.

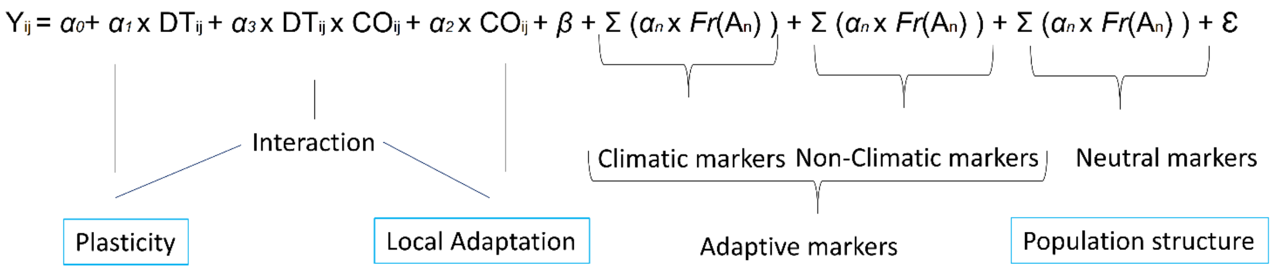
3.4. Drivers of global trait variation of natural selection at wide-rage scales.

Intra-specific trait variation is the result of local adaptation and phenotypic plasticity, and the research activities reported before are focused on the study of these processes in shaping species ranges under current and new climate conditions. Natural selection is the main process that has shaped intra-specific trait variation over generations, and understanding which were the main (climatic) drivers of natural selection in the past is useful to understand how natural selection would handle new patterns of local adaptation in the future (Lafontaine *et al.*, 2018).

Detecting climate change-driven natural selection is the next natural step to understand the evolutionary potential of organisms under climate change. Over generations, different climatic drivers could have driven natural selection at wide-range scale. For example, geographical acclimation patterns of plant respiration seem to respond to warming drivers (Reich *et al.*, 2016), whereas precipitation and evapotranspiration seem to explain higher intra-specific trait variation than temperature (Siepielski *et al.*, 2017). Likewise, extreme climate events are promoting directional selection and hence local adaptation of populations, already evident in populations suffering marginal climatic extremes (Exposito-Alonso *et al.*, 2018). Understanding whether precipitation, temperature, or evapotranspiration or a combination of all of them have been the main drivers of local adaptation in the recent past would help us to anticipate which populations could be more at risk under new projected climates.

The fast development of genomics allow us to build genome maps of allelic selection differentials that can be linked with trait values (Bay *et al.*, 2018; Brancalion *et al.*, 2018; Ruegg *et al.*, 2018). In addition, for some species, genomic data has been analyzed from provenance tests in which we can identify the origin of the material, allowing us to investigate together the role of inter- (differences in local adaptation and phenotypic plasticity) and intra- (evolutionary potential) populations' variation of relevant adaptive traits related with fitness (e.g. tree height and survival) at wide-rage scale.

With Juliette Archambeau's PhD project we propose to merge into single models phenotype, genotype and environment in the following equation:



$$Y_{ij} = \alpha_0 + \alpha_1 \times DT_{ij} + \alpha_3 \times DT_{ij} \times CO_{ij} + \alpha_2 \times CO_{ij} + \beta + \underbrace{\Sigma\,(\alpha_n \times Fr(A_n))}_{\text{Climatic markers}} + \underbrace{\Sigma\,(\alpha_n \times Fr(A_n))}_{\text{Non-Climatic markers}} + \underbrace{\Sigma\,(\alpha_n \times Fr(A_n))}_{\text{Neutral markers}} + \varepsilon$$

Y = Phenotypic trait value
CT = Climate of the trial
CO = Climate of the provenance
β = random effects
ε = error

The compilation of individual phenotypic data performed in the last years (see the "Activity report" section) together with the genomic information obtained for the same populations including allele frequencies of relevant candidate genes for adaptation, as well as information on standing gene pools and associations between genotypes and phenotypes (GWAS) will allow us to start with this ambitious research topic. We will start with two ecologically contrasted widespread *Pinus* species in Europe: *Pinus sylvestris*, with the largest tree distribution in Europe and Asia, and *Pinus pinaster*, which distribution covers the Western Mediterranean basin and Atlantic front from North Africa to France. The final goal will be to development new species distribution models that account for local adaptation, plastic responses and the evolutionary potential of populations across their ranges based on genomic data (available and newly generated), using novel multi-trait, multi-loci GWAS approaches.

Main collaborators: Santiago González-Martínez (BIOGECO).
Students associated: Juliette Archambeau (PhD 2018- 2021);
Funding: GENTREE and B4EST (H2020)

3.5. Anticipating the ecological communities of the future & adapting trees for the future

I will continue applying as much as possible fundamental research to the real world as I described in the last section of the activity section. ΔTraitSDM based in multiple trait variation over large geographical scales open a new perspective to generate new translocation scenarios based in a more complete set of fitness-related traits, particularly those related with reproduction.

In the near future, I will continue providing my models to any research institute or conservation organization that can benefit from these approaches for decision making and as conservation tools. ΔTraitSDM predictions can help to identify relevant tree traits that are under significant local adaptation and use this information to identify those populations that would be adapted to future climates based on different traits and trait combinations. Likewise, our models can be used to identify target populations for the conservation of forest genetic resources and the translocation of biological material to enhance population adaptation to a rapidly changing climate. Genetic Conservation Units (GCU) have been designed for the main tree species in Europe to assure the maintenance of evolutionary processes within populations (Koskela *et al.*, 2013). In collaboration with the European Forest Genetic Resources Programme (EUFORGEN), we can use our models to evaluate how the GCU network of forest trees will be affected by climate change, and which combinations of traits tend to render beech GCUs particularly susceptible or resilient to climate change. For those populations whose persistence will be rendered difficult by climate change in the near future, translocation scenarios for forest trees based on the most important traits defining tree fitness across the distribution ranges can be generated in collaboration with the European Forest Institute (section EFI Atlantic).

Main collaborators: Michele Bozzano (EFI Biodiversy International); Christophe Orazio (EFI-Atlantics); Annabel Porté (BIOGECO).

Students and Postdocs associated: Alexandre Changenent (PhD 2017- 2020);

Funding: Project Region Aquitaine Athene, NETTREE H2020 (under development)

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