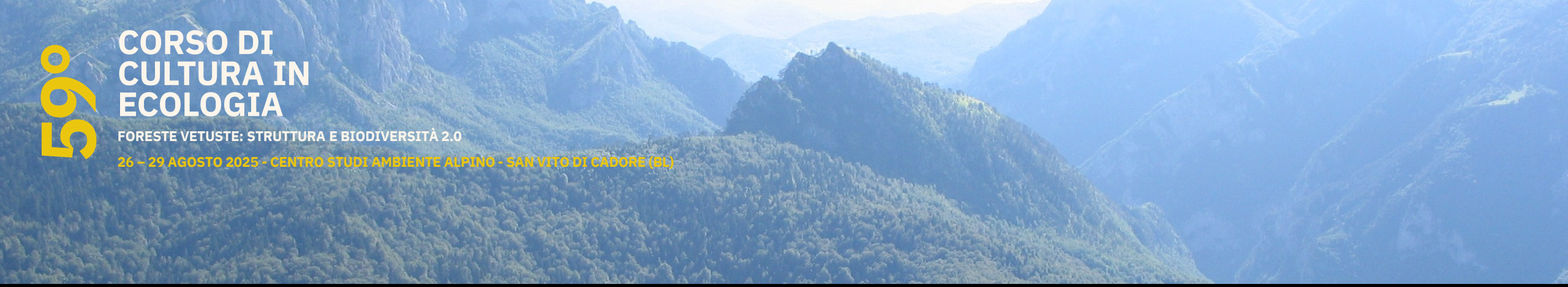


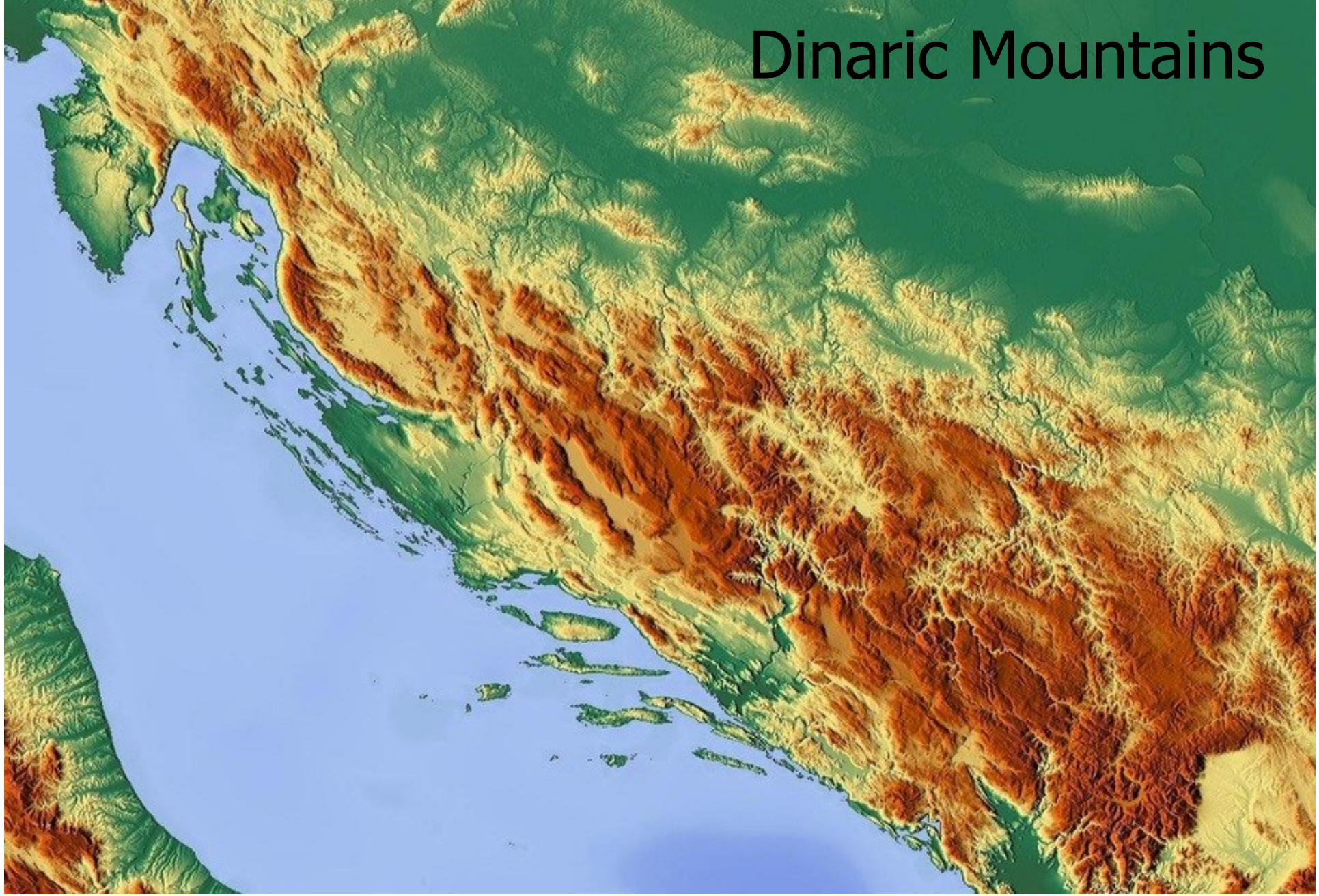
CORSO DI CULTURA IN ECOLOGIA

FORESTE VETUSTE: STRUTTURA E BIODIVERSITÀ 2.0

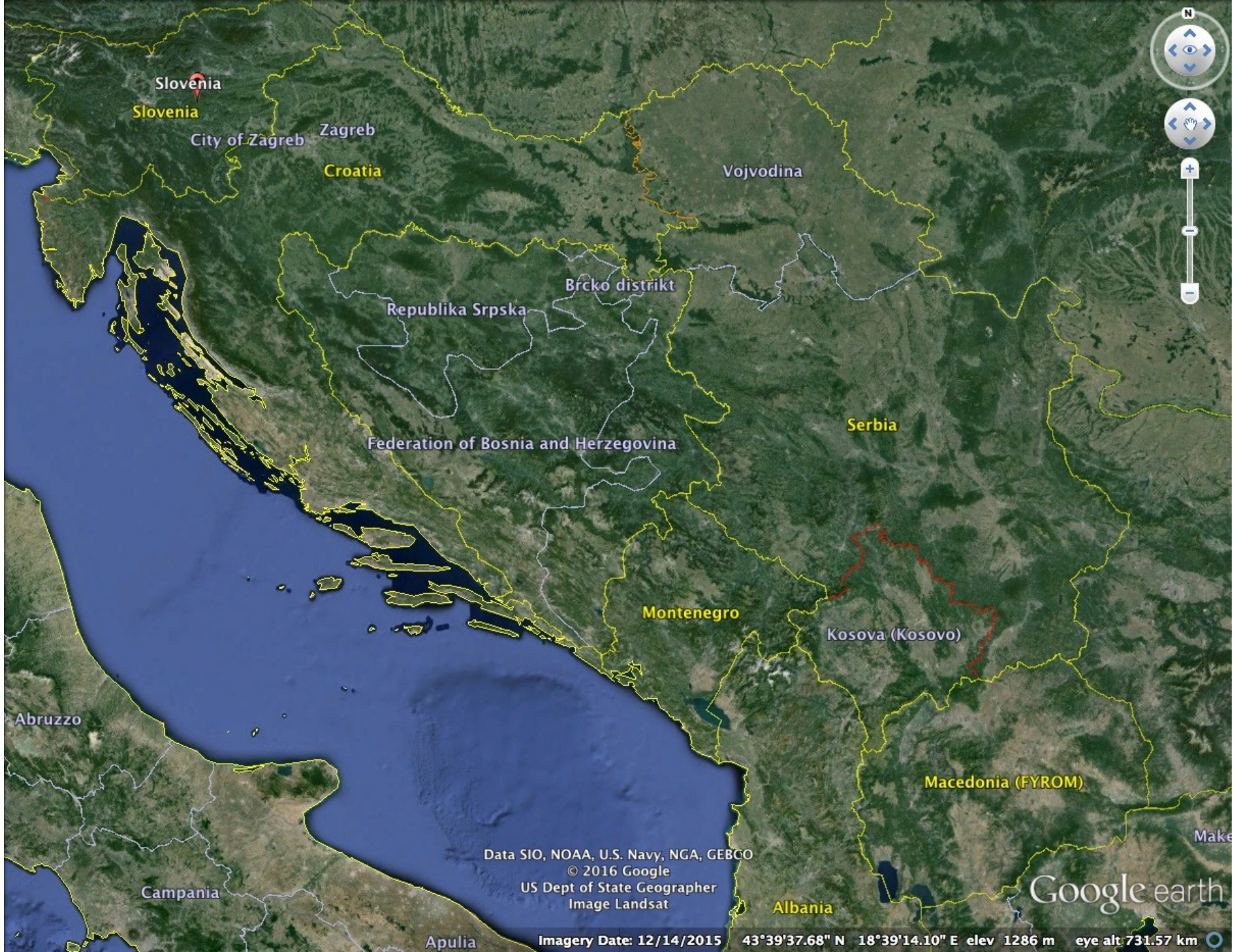
26 – 29 AGOSTO 2025 - CENTRO STUDI AMBIENTE ALPINO - SAN VITO DI CADORE (BL)

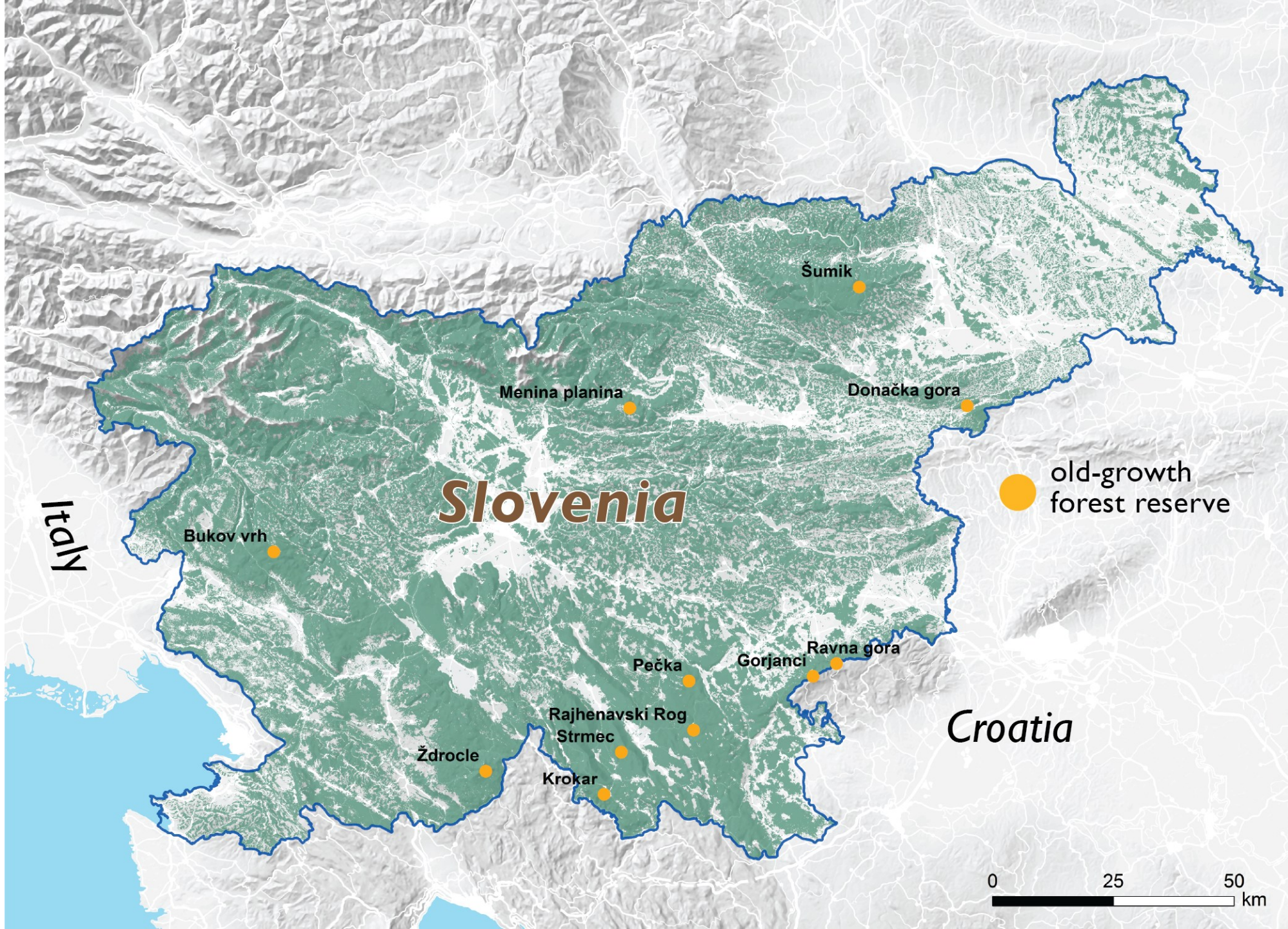
# Scientific and conservation insights from old-growth forests in the Dinaric mountains and beyond

Tom Nagel, University of Ljubljana




600 Km long and 150 km wide; Mesozoic rocks, mainly limestone and dolomite

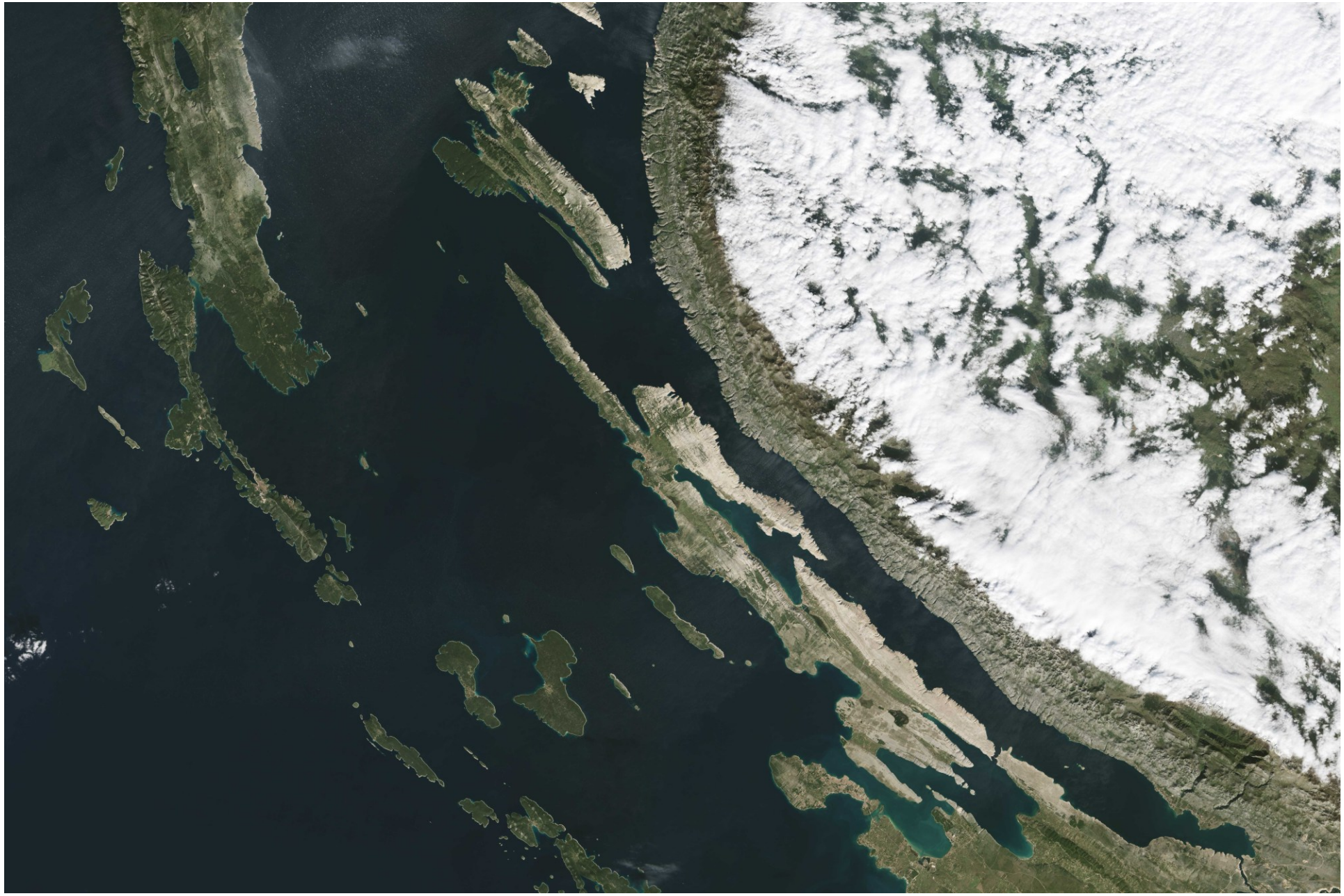

Slovenia
Slovenia
City of Zagreb
Zagreb
Croatia
Vojvodina
Brcko distrikt
Republika Srpska
Federation of Bosnia and Herzegovina
Serbia
Montenegro
Kosova (Kosovo)
Macedonia (FYROM)
Albania
Abruzzo
Campania
Apulia
Data SIO, NOAA, U.S. Navy, NGA, GEBCO
© 2016 Google
US Dept of State Geographer
Image Landsat
Google earth
Imagery Date: 12/14/2015 43°39'37.68" N 18°39'14.10" E elev 1286 m eye alt 731.57 km

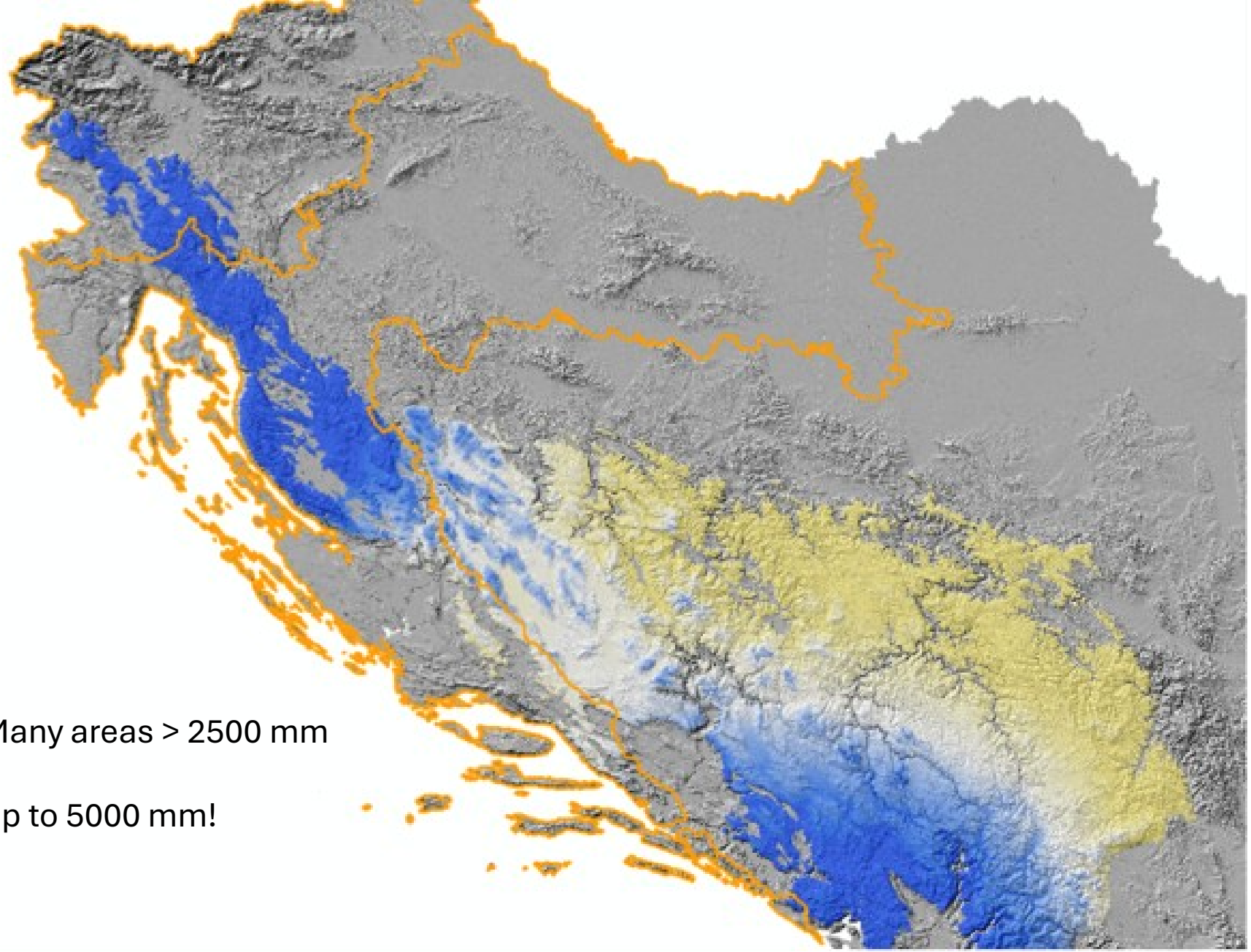

Slovenia
Italy
Croatia
Šumik
Menina planina
Donačka gora
Bukov vrh
Ravna gora
Gorjanci
Pečka
Rajhenavski Rog
Strmec
Ždrocle
Krokar
old-growth
forest reserve
0
25
50
km

“Karst” geomorphology

- Limestone is very deep (1-3 km)
- Pronounced relief
- Globally unique in the diversity and density of these features
- Formed by water and chemical dissolution of carbonate rocks

# Climate



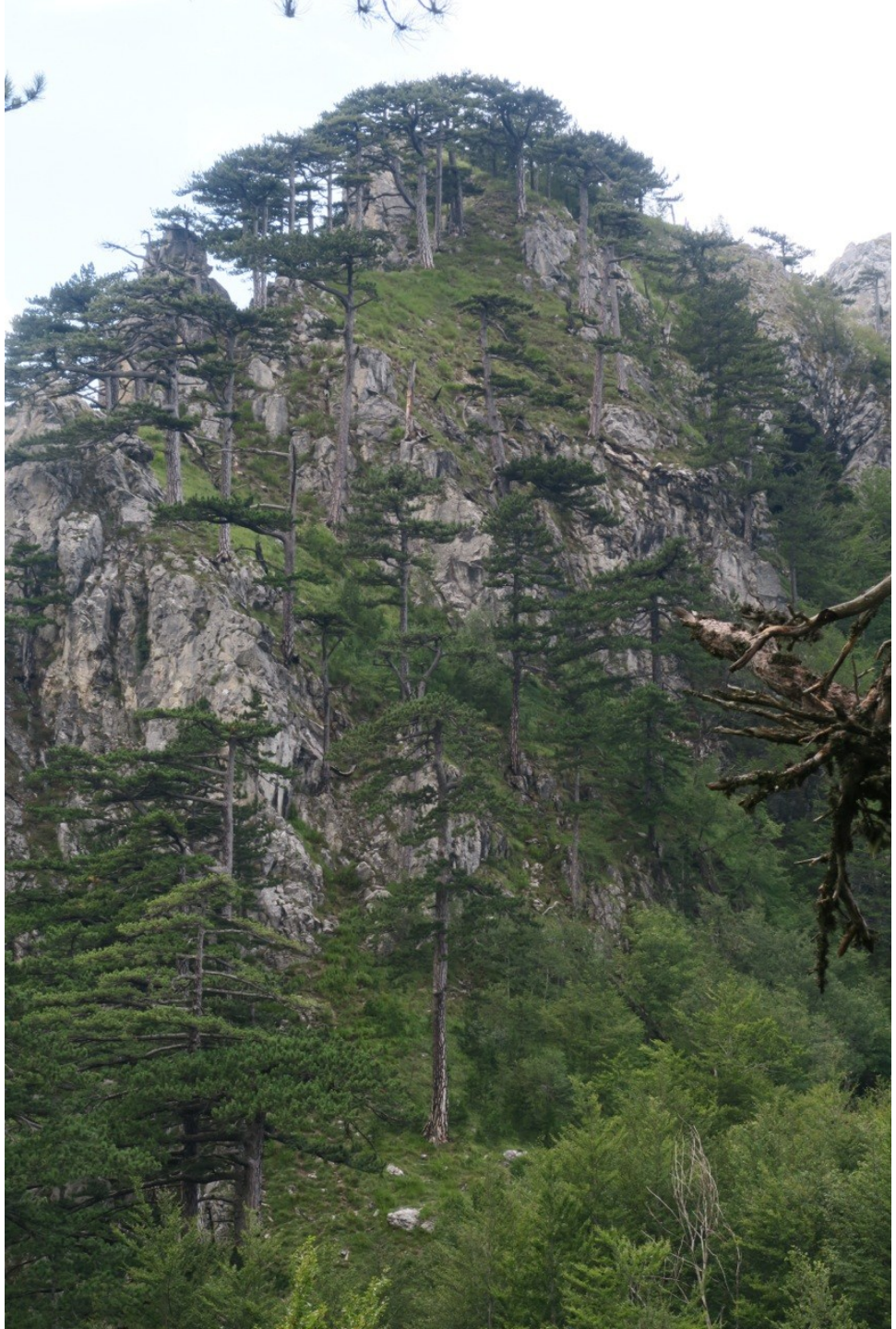



Average annual precipitation (mm) over past 50 yrs (blue > 1500mm - yellow 800 mm)

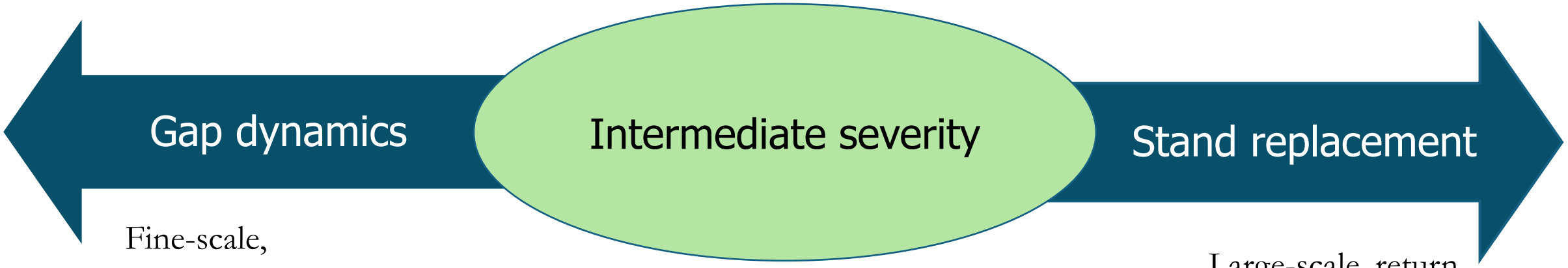
*Fagus sylvatica*

*Abies alba*

*Acer pseudoplatanus*
*Fraxinus excelsior*
*Ulmus glabra*



# Conceptual model of temperate forest disturbance regime



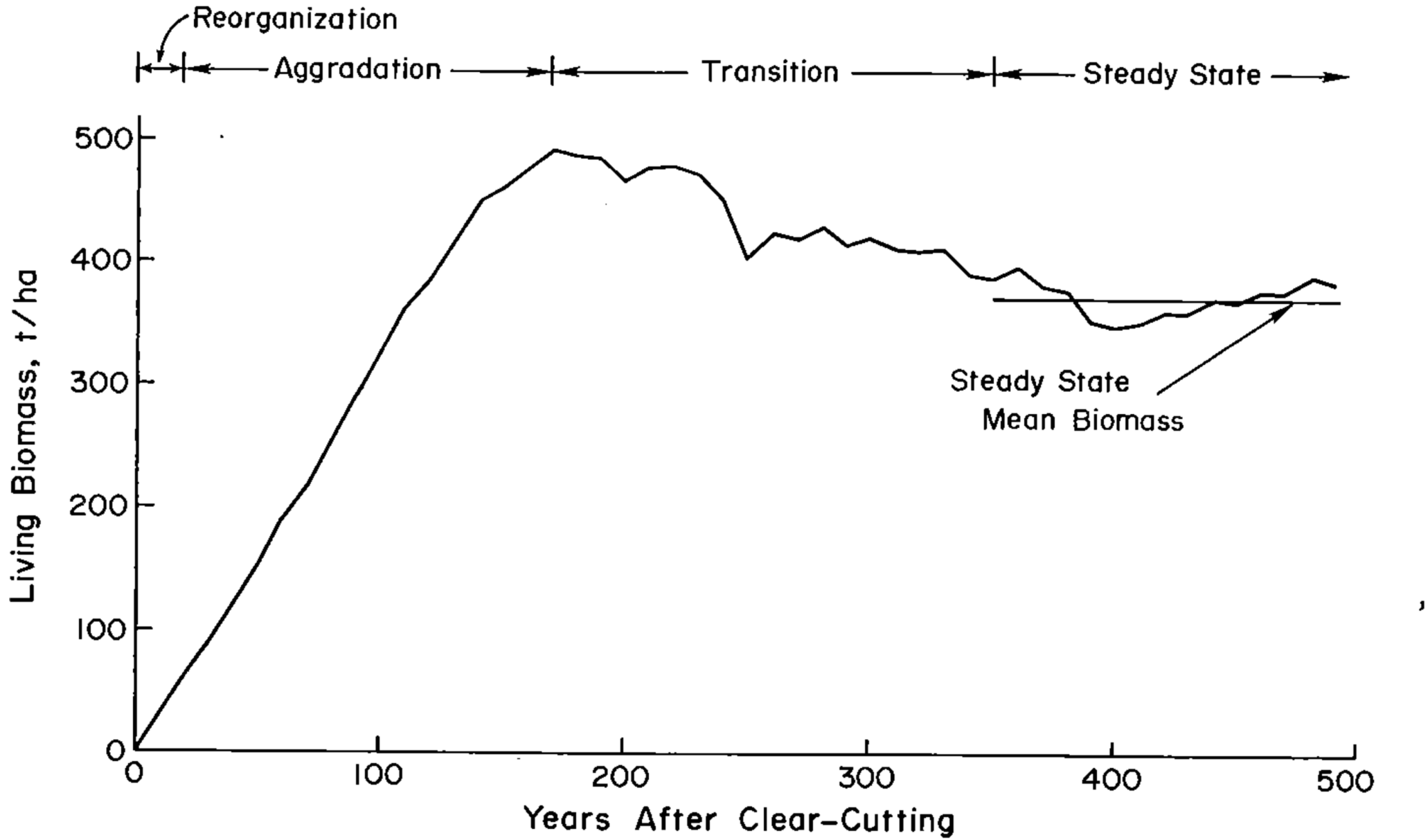

Fine-scale, continuous process

Intermediate-scale and severity, return interval less than tree longevity

Large-scale, return interval several thousand years

The traditional conceptual model in temperate old-growth forests in Europe and the N. America was that "gap-phase" processes drive community dynamics, in that tree replacement occurs under regimes of low-intensity, diffuse, relatively constant disturbance

- basically assumes equilibrium forest structure and composition at stand scales
- such processes are sufficient to maintain tree species composition

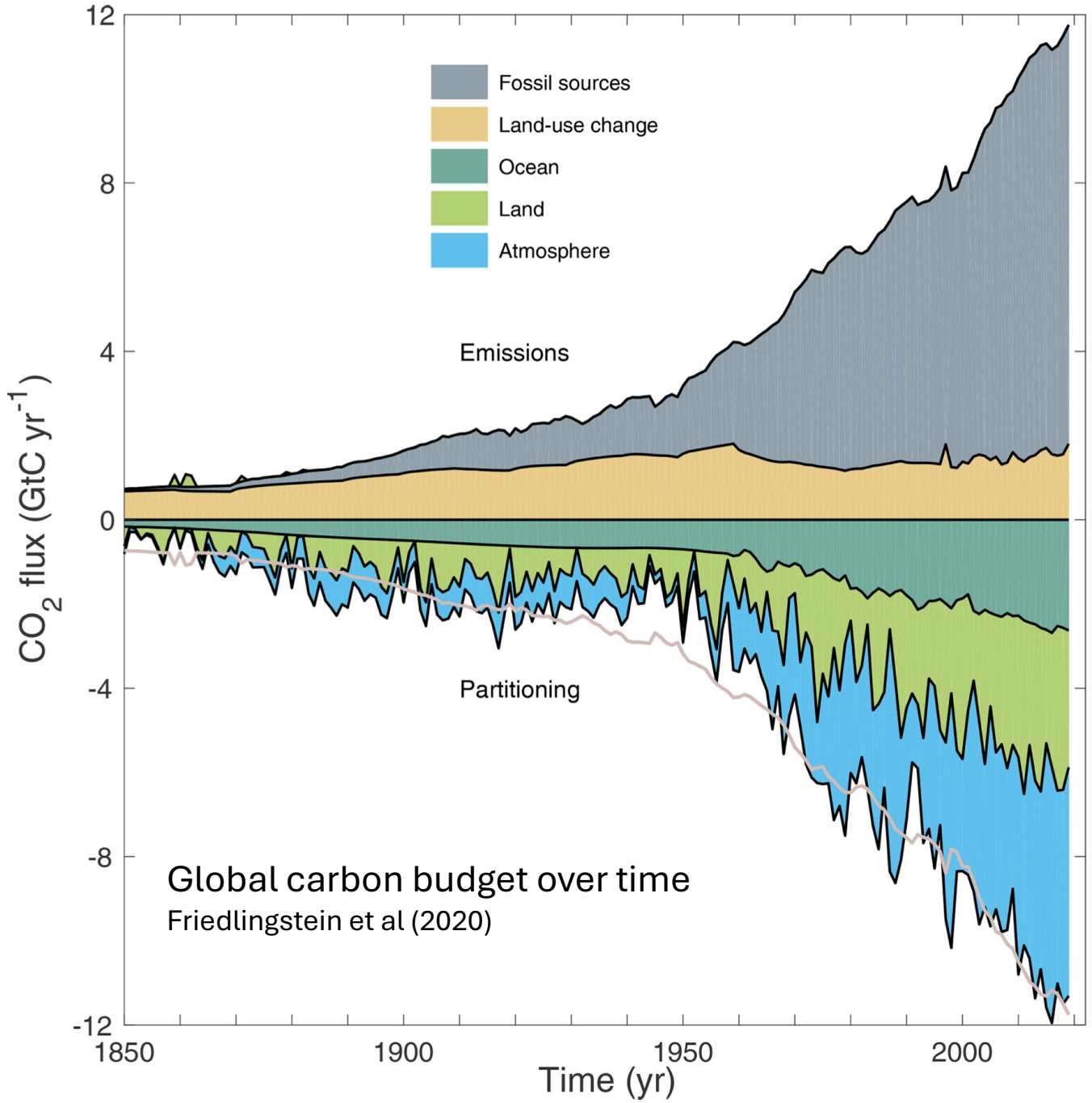



Bormann and Likens, 1979

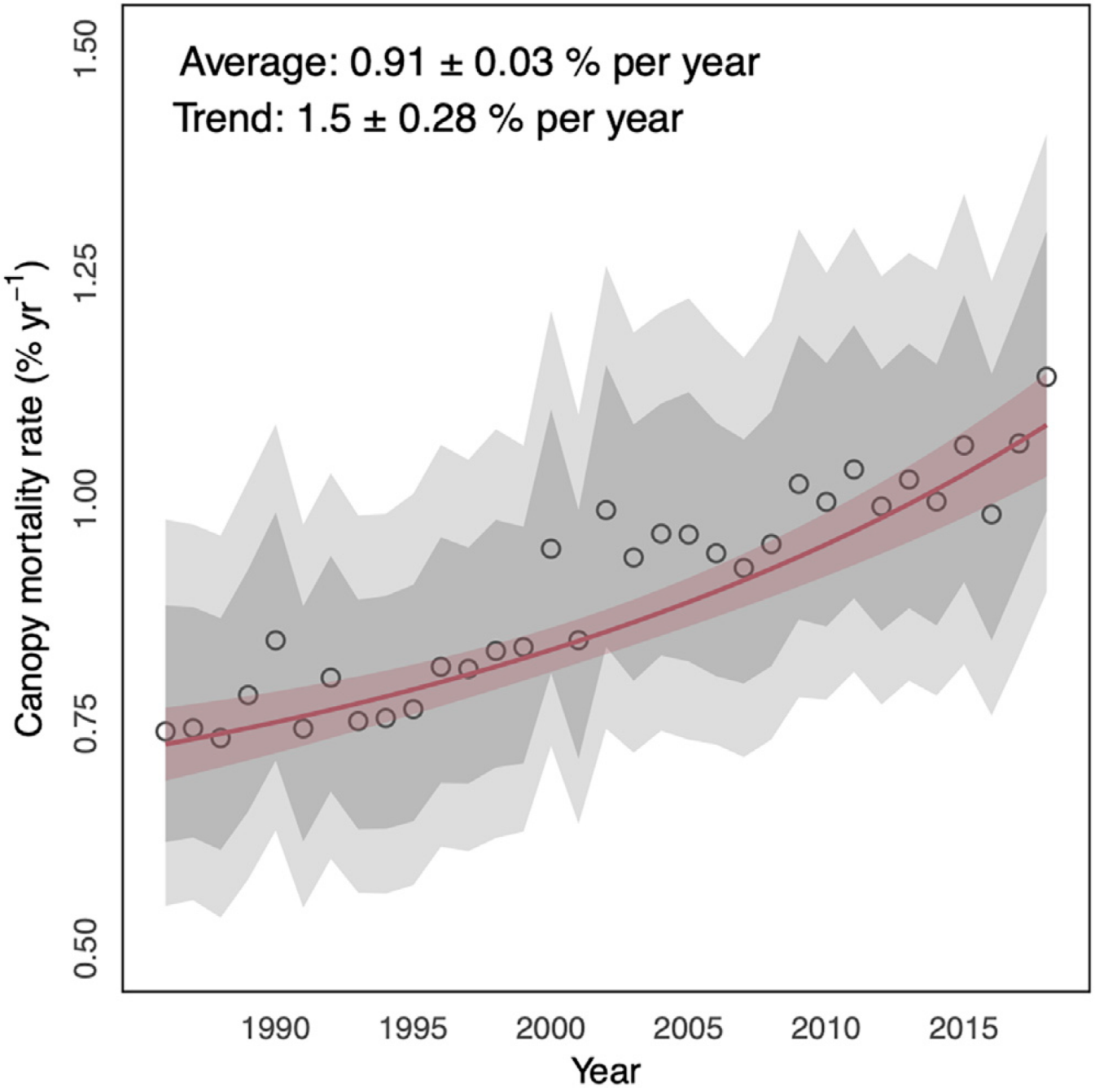
What about carbon and forest reserves?

- Carbon cycle:

$C_{storage} = C_{uptake} - C_{respiration} - C_{mortality}$



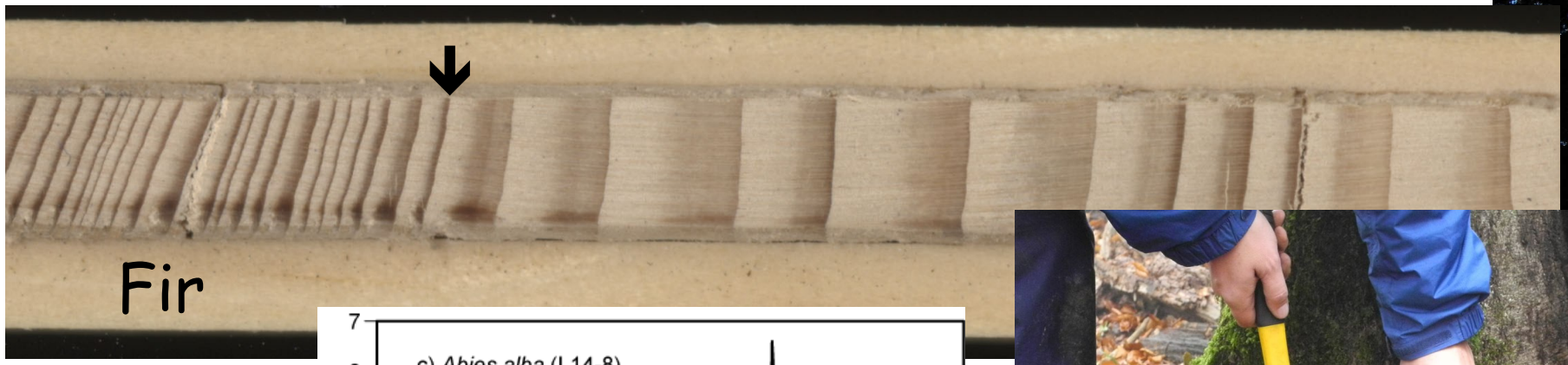
- Increasing rates of canopy mortality in managed forests of Europe

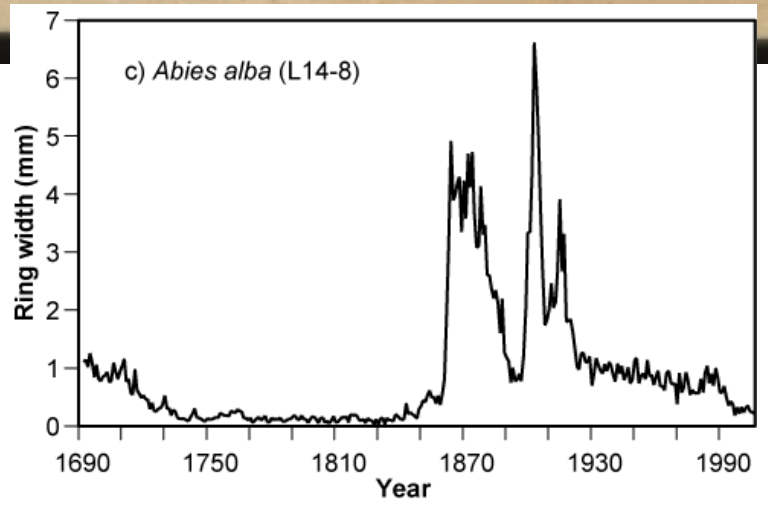



Senf et. al. One Earth, 2021

# Methods for studying disturbance and dynamics in old-growth forests

- Direct observations of recent disturbances
- Canopy gap studies
- Dendroecological studies
- Permanent plots

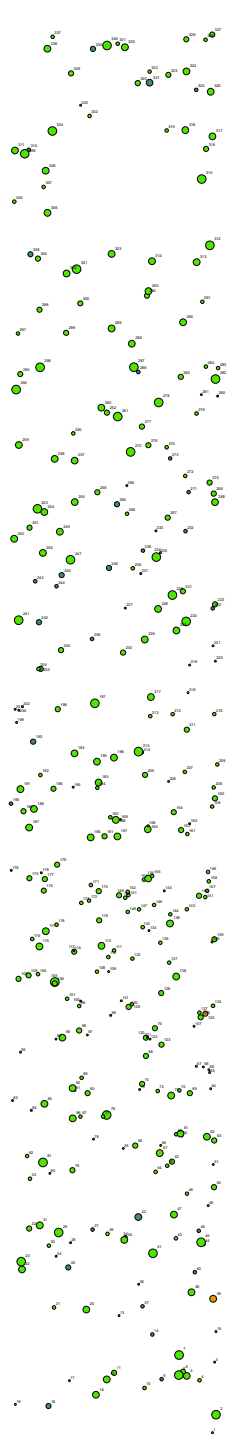



# Permanent plot network

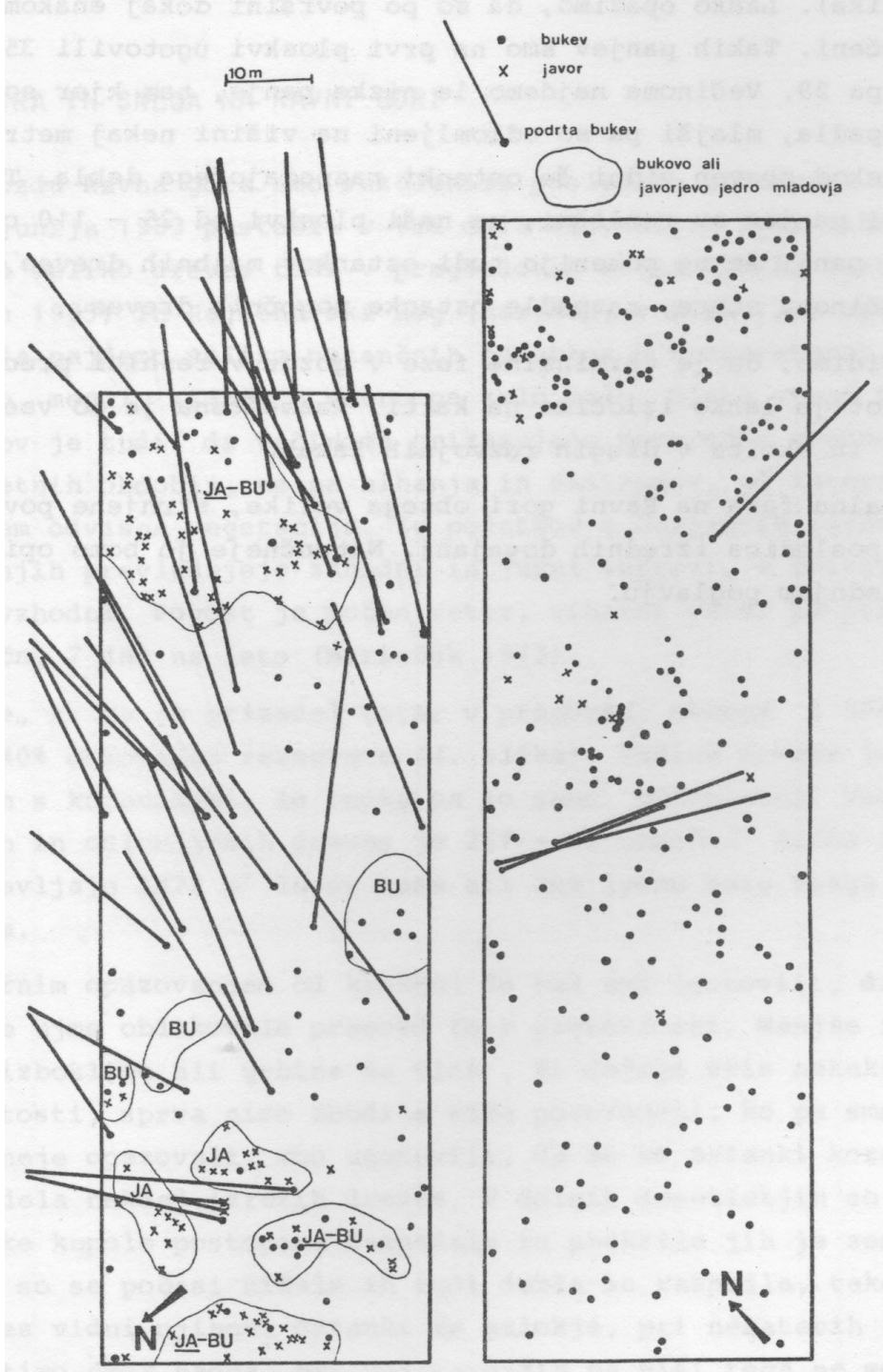
- 11 old-growth reserves
- Total of 20 plots, 13 ha
- Established around 1980
- Plots established across a range of “development phases”
- All trees ≥ 5 cm d.b.h. tagged, measured and mapped
- Re-measurements include d.b.h, mortality, and mode of mortality
- New recruits that reach the d.b.h. threshold are tagged and mapped at each census
- Census interval is 5 year intervals

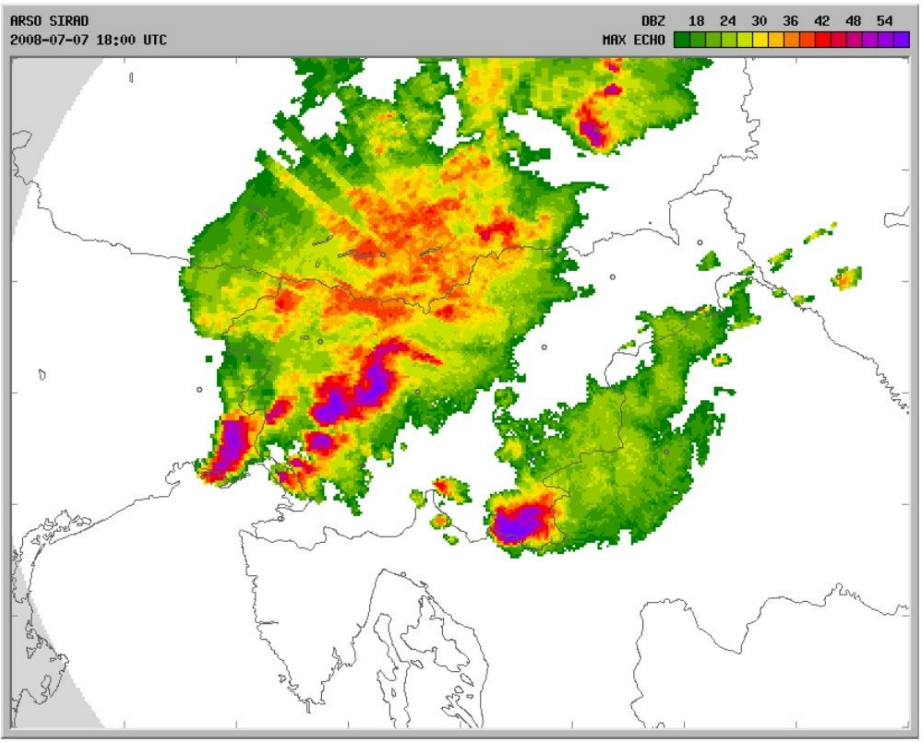
- Biomass calculated from species specific allometric equations (R package allodb, Gonzalez-Akre et al.)

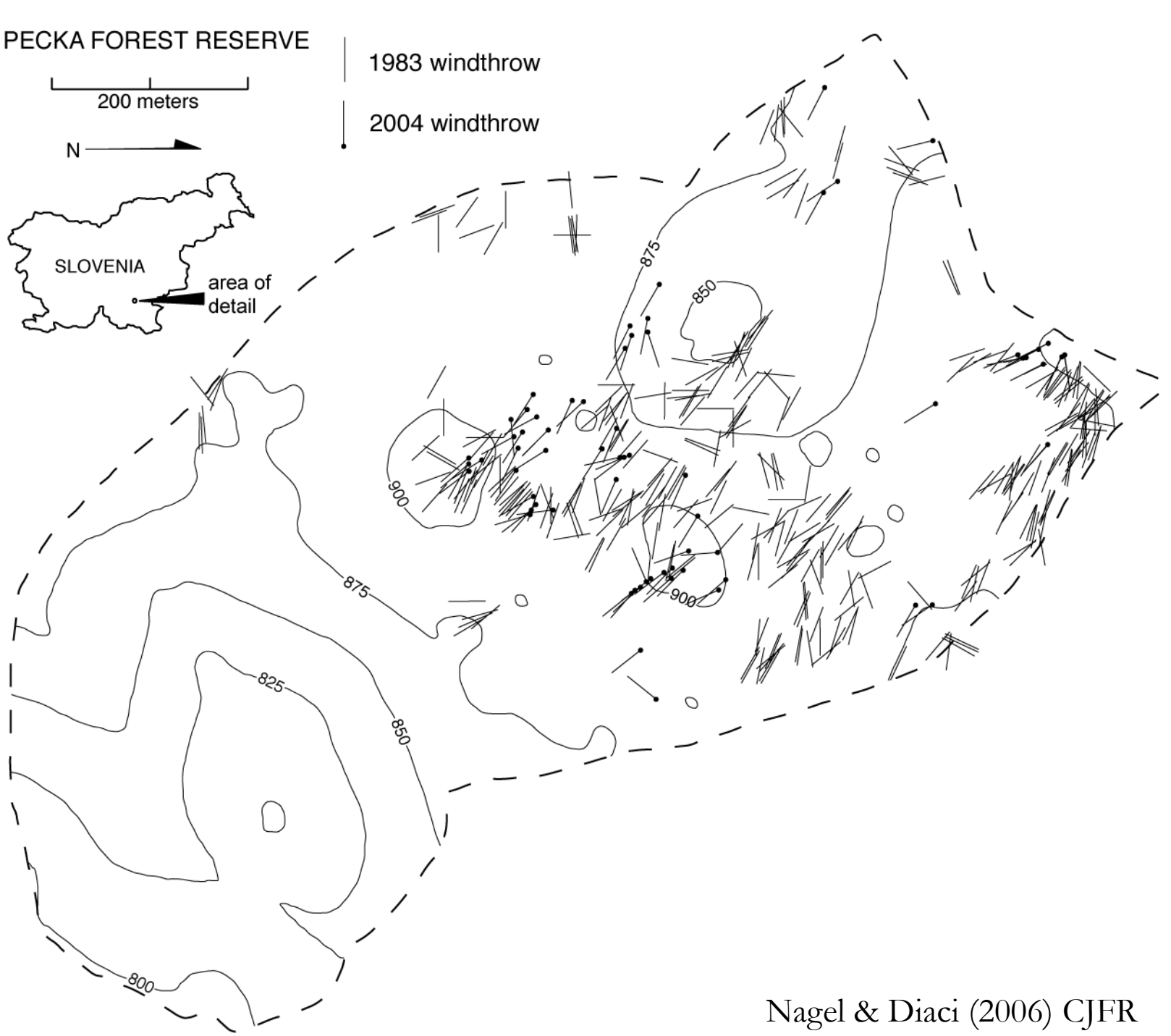


Ravna Gora forest Reserve
Windthrow in 1983

Deadwood input: 437 m3/ha



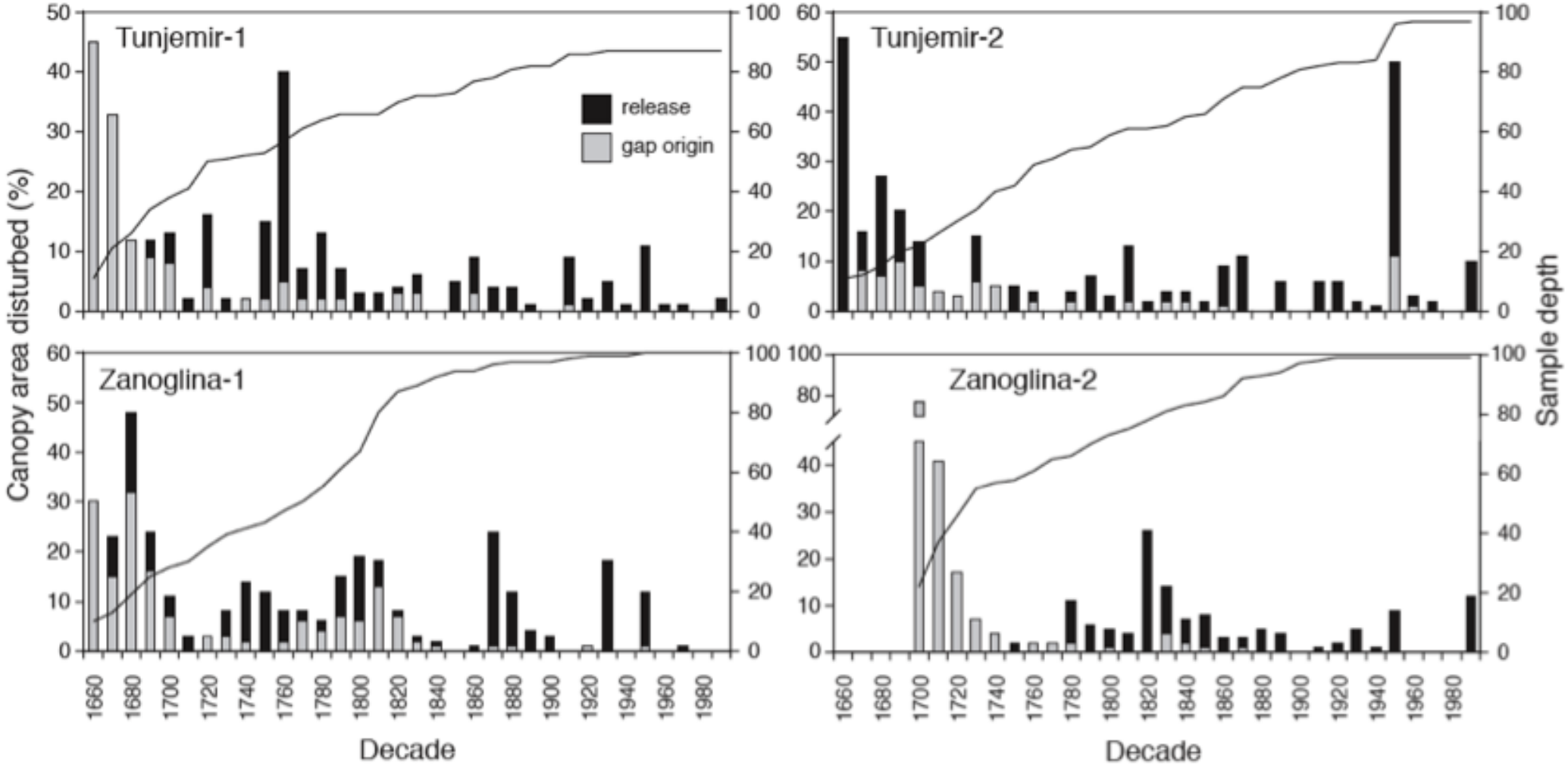



Combined mortality of both storms equal to a decade of baseline mortality recorded in permanent plots

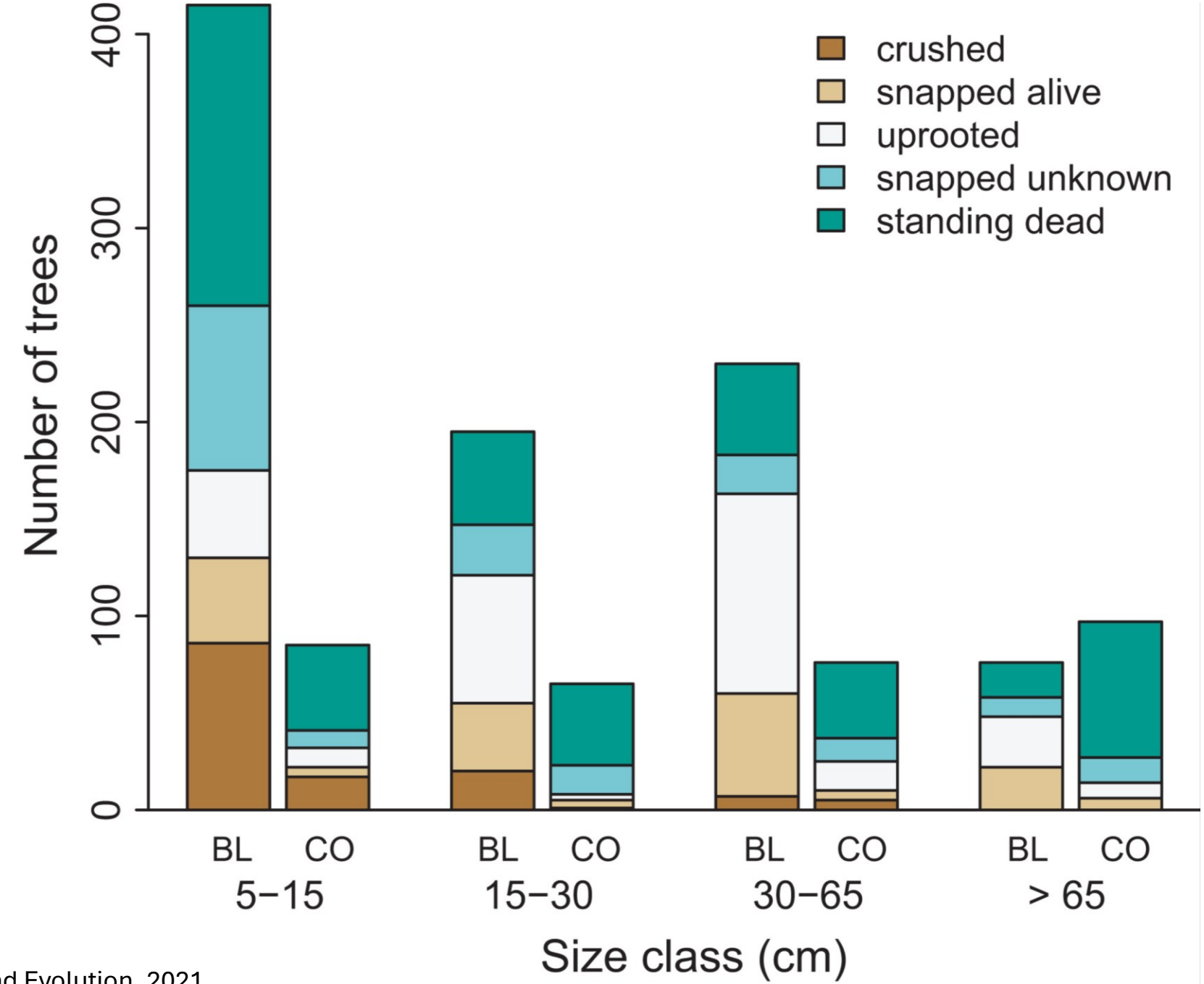
Nagel & Diaci (2006) CJFR

# Dendroecological reconstruction of disturbance history in 4 stands in Peručica, BiH

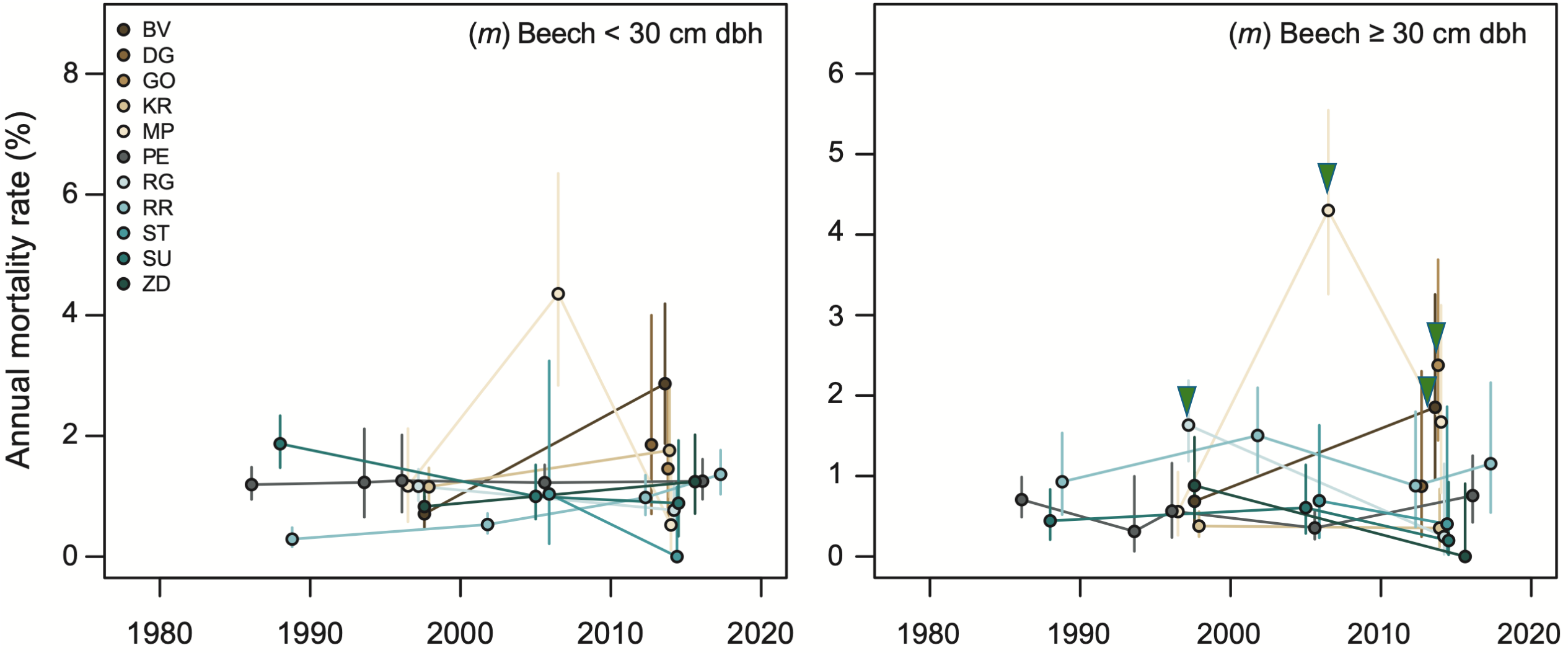



Disturbances that remove 30-50% of the canopy recur approx every 150-450 years

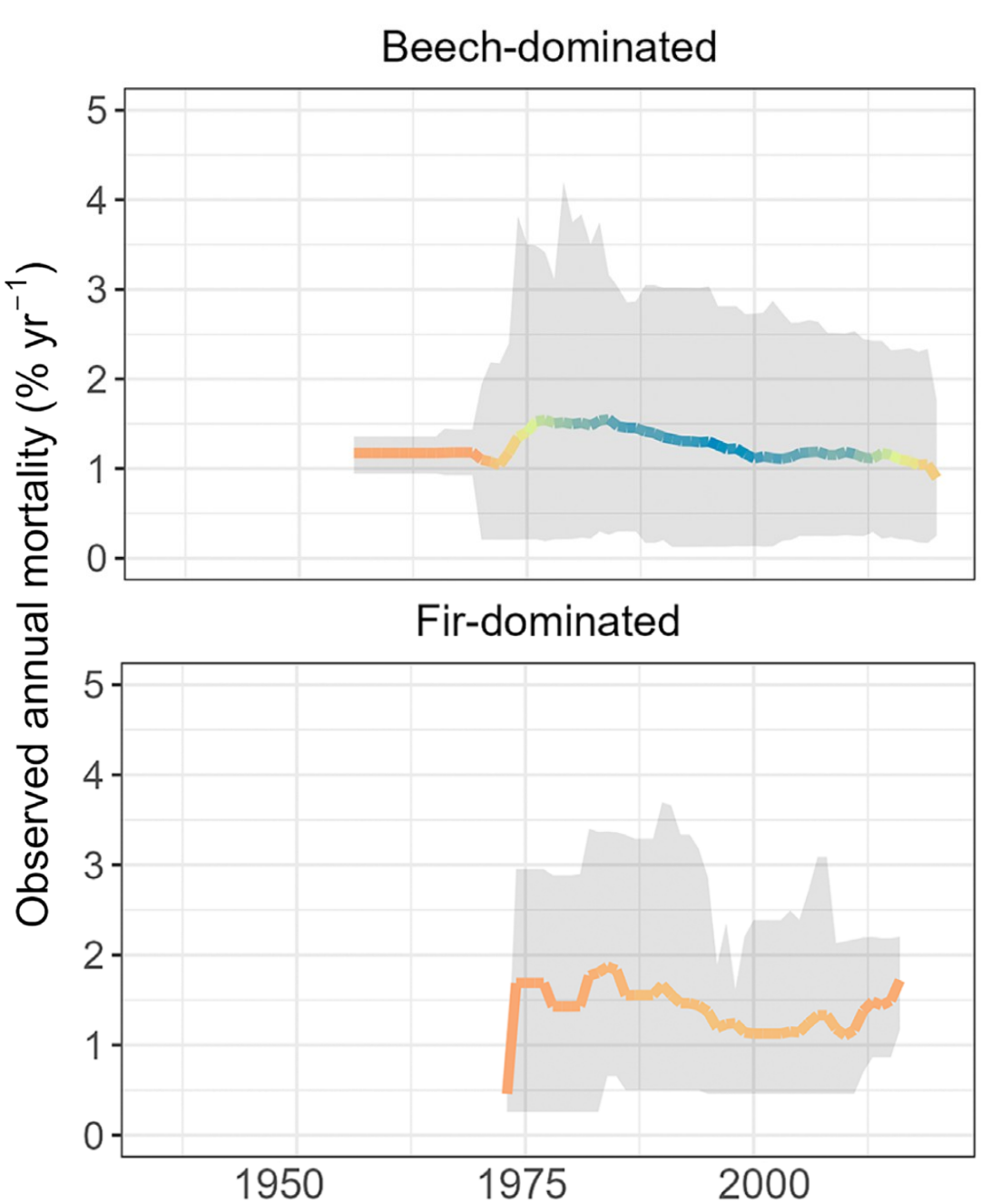
Nagel et al. (2014) Ecological Applications

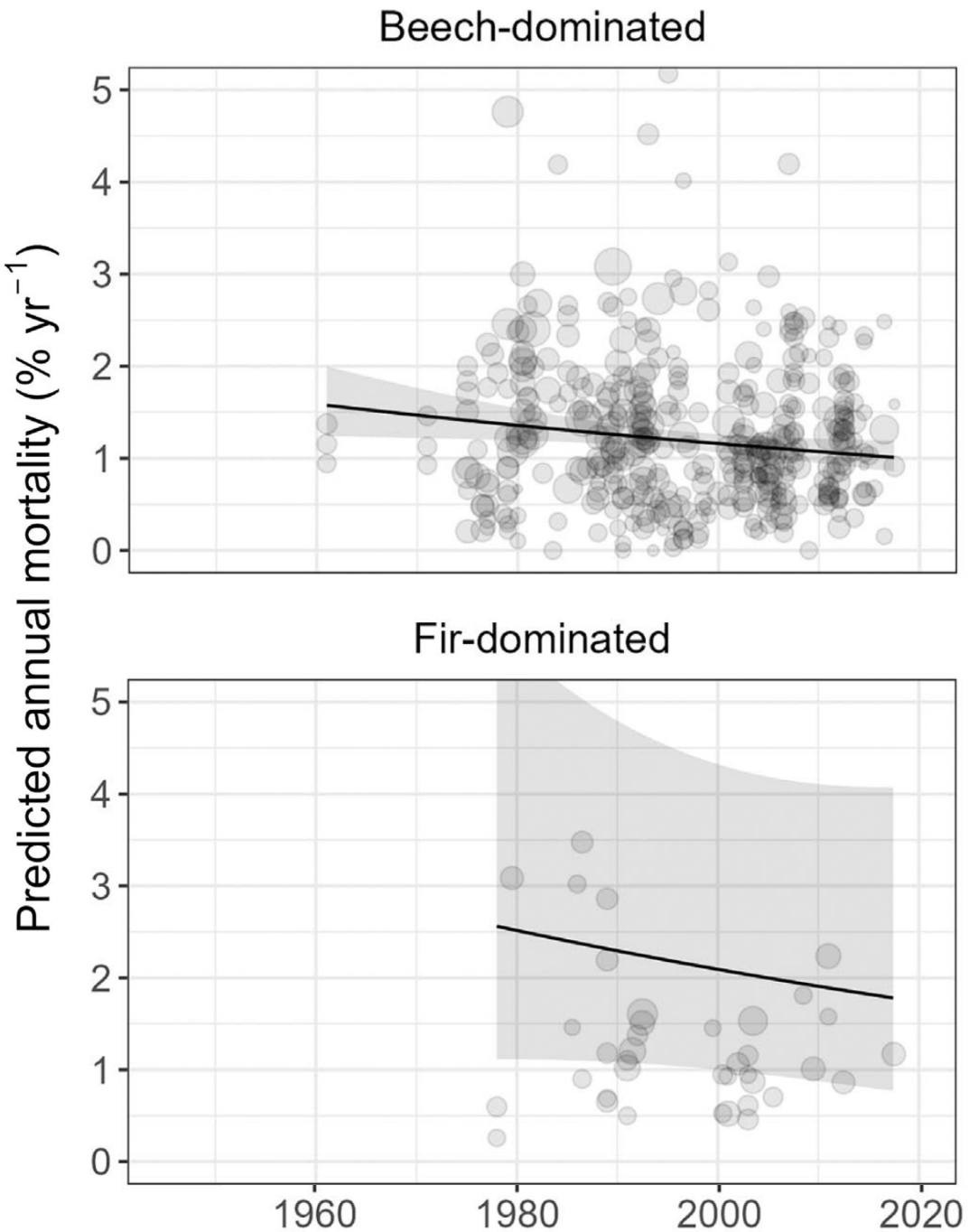



Nagel et. al. Ecology and Evolution, 2021

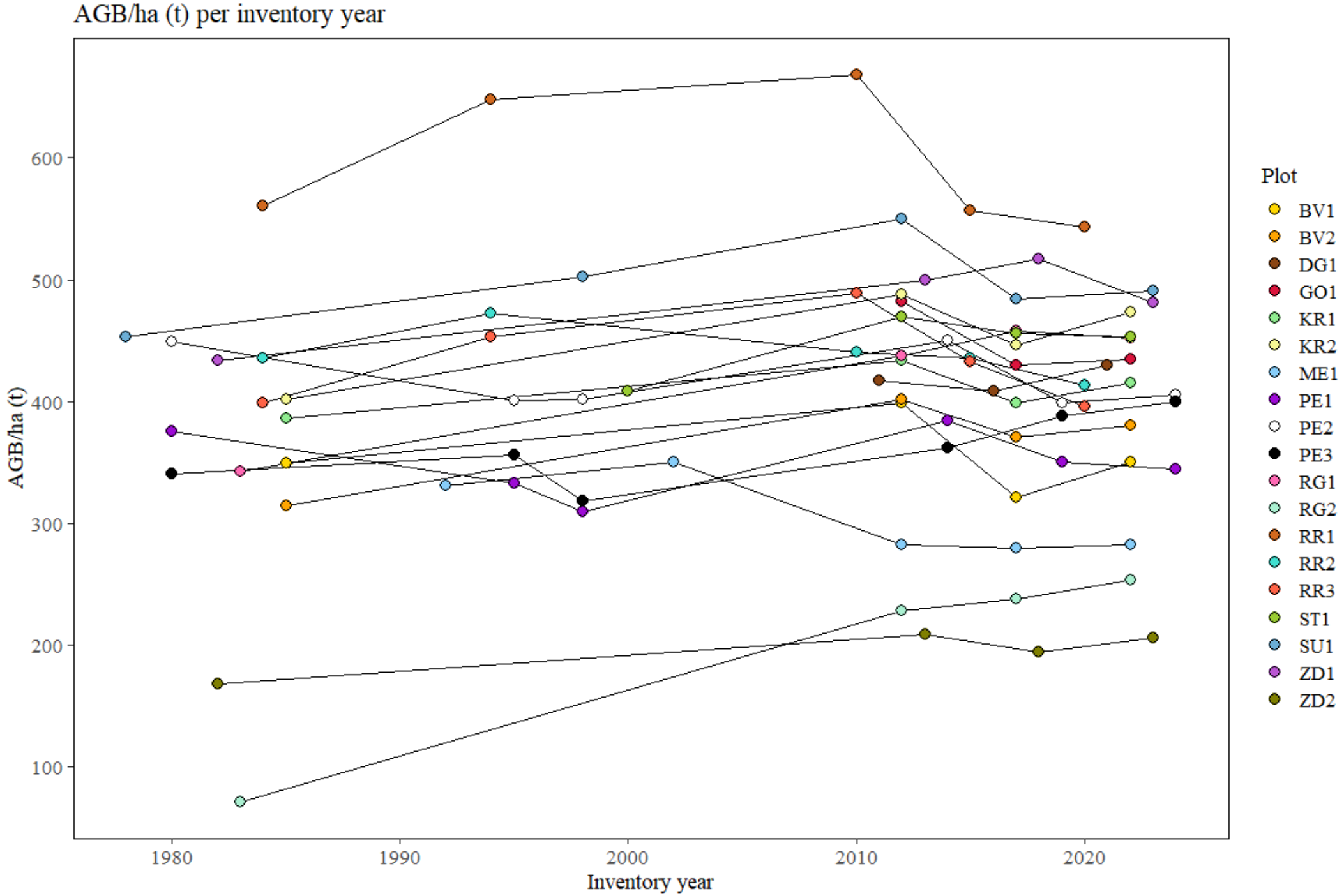


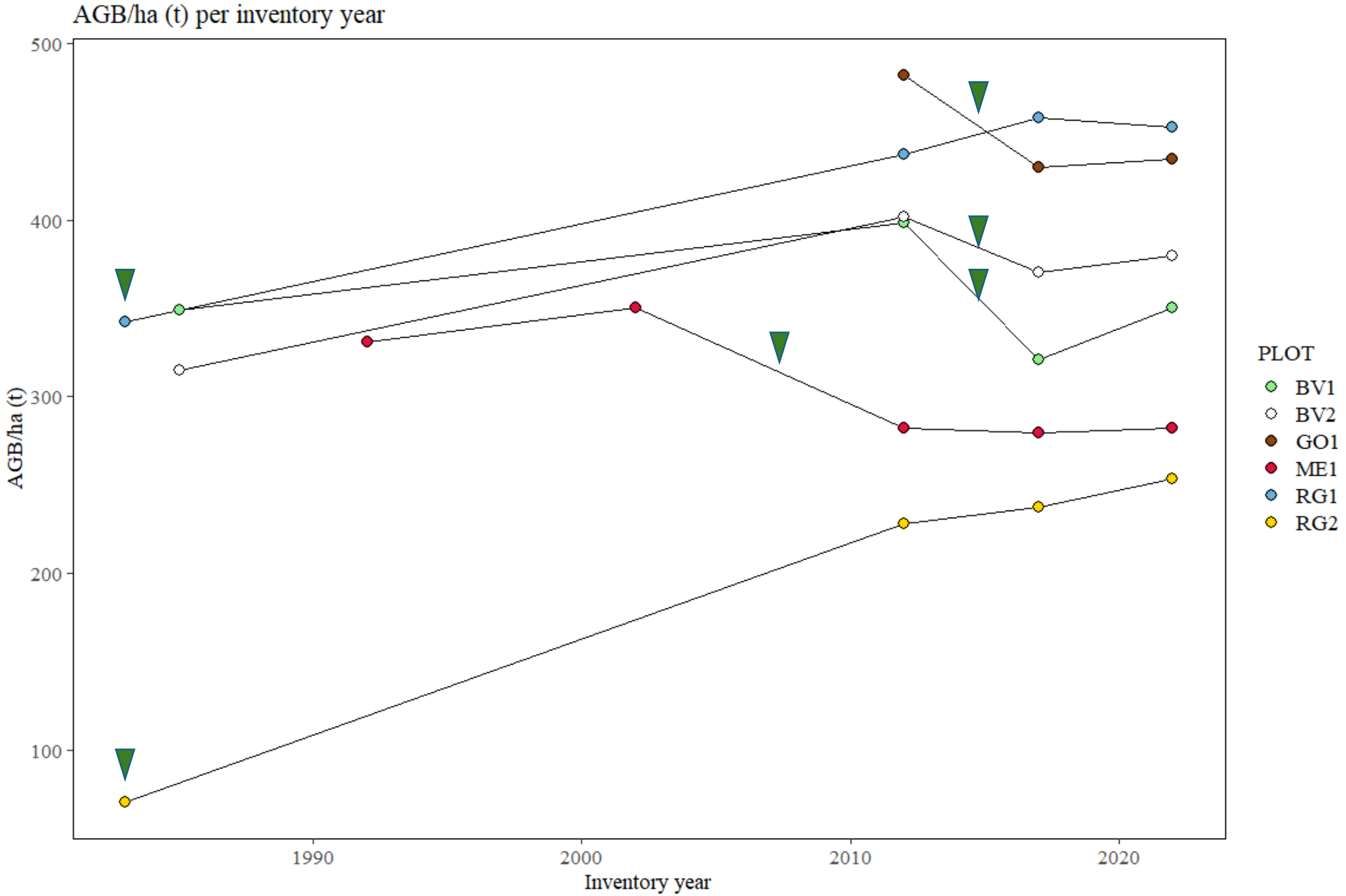

Nagel et. al. Ecology and Evolution, 2021

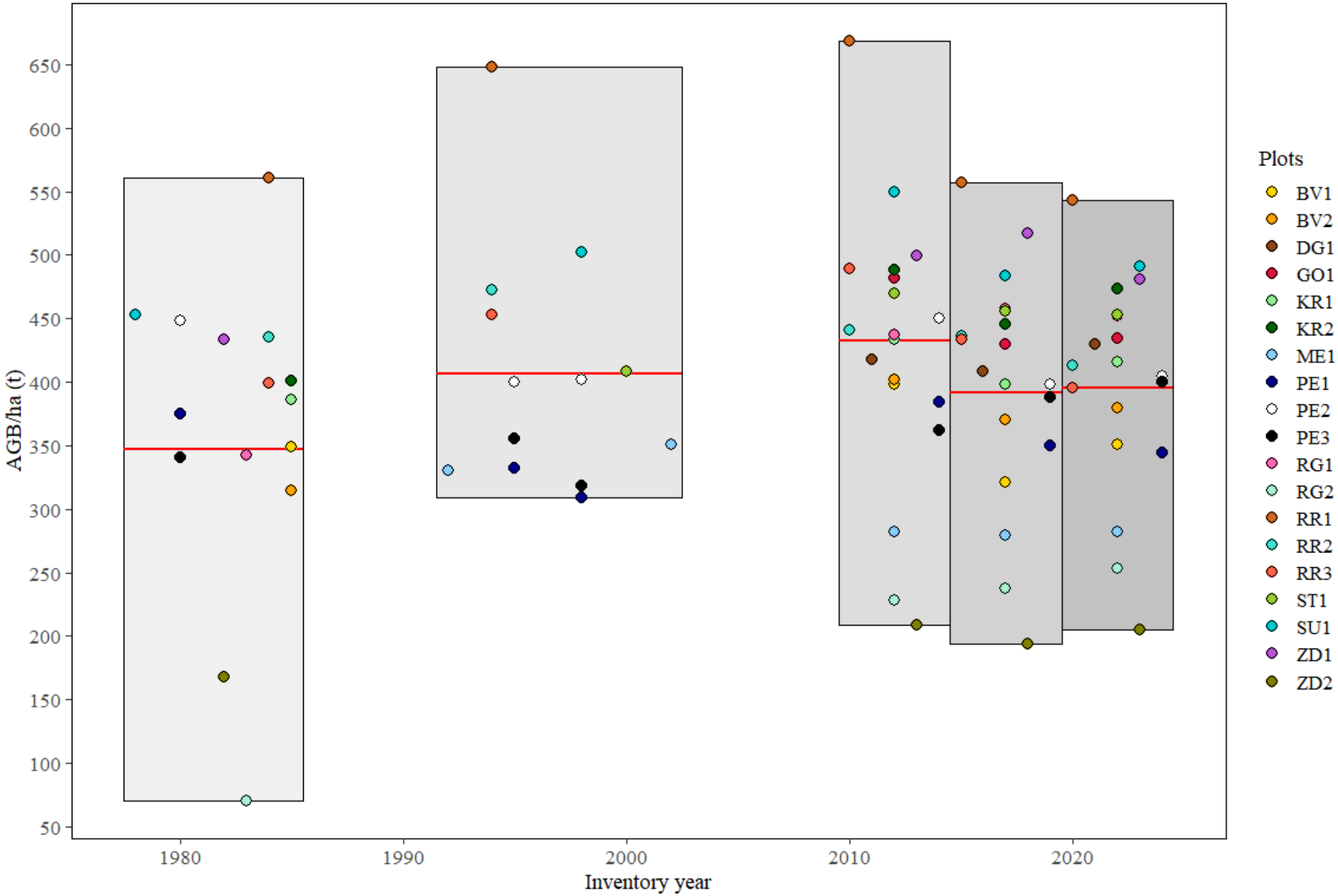


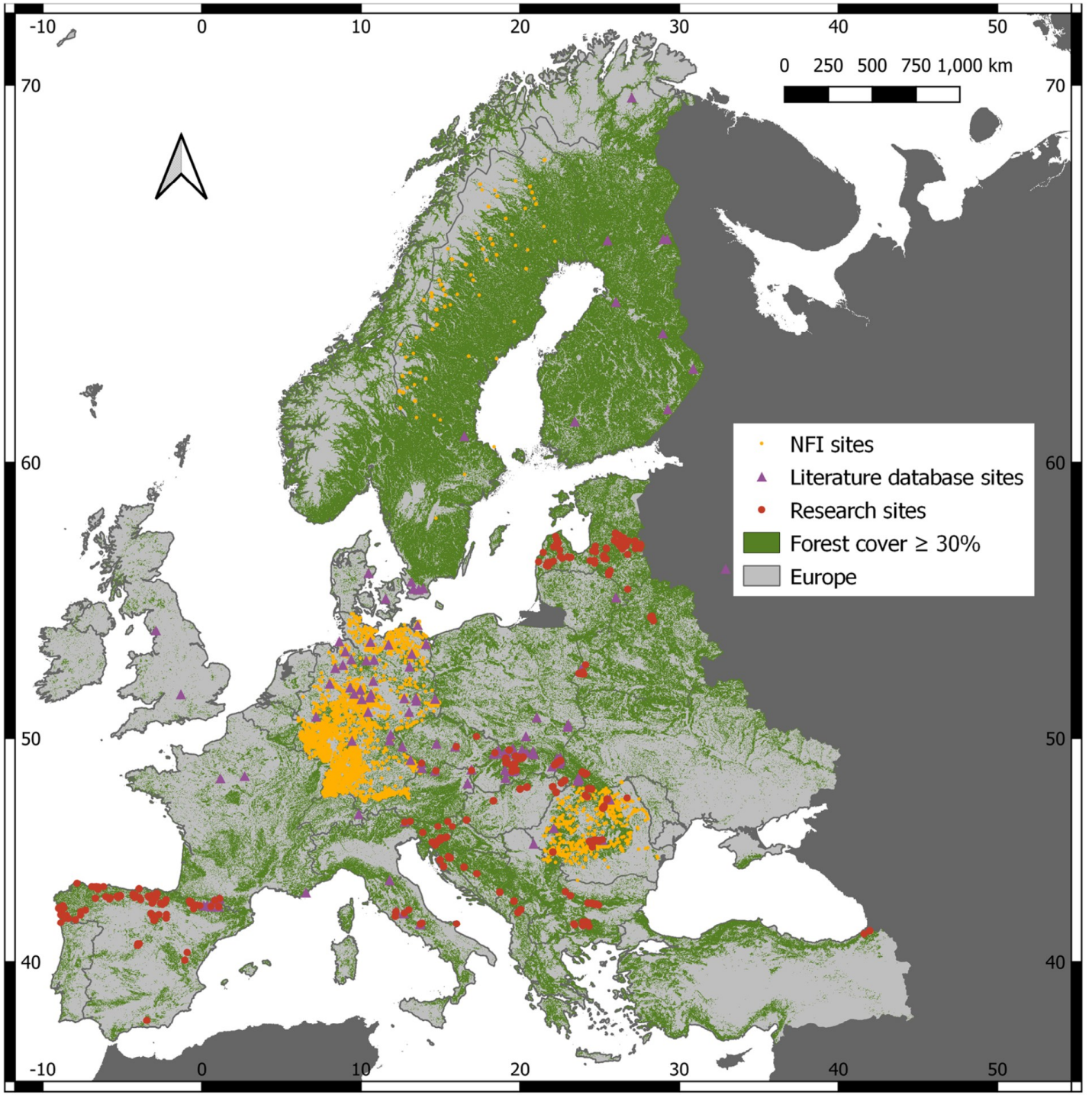

Idoate-Lacasia et. al., 2025, J of Ecology


AGB/ha (t) per inventory year
AGB/ha (t)
600
500
400
300
200
100
1980
1990
2000
2010
2020
Inventory year
Plot
BV1
BV2
DG1
GO1
KR1
KR2
ME1
PE1
PE2
PE3
RG1
RG2
RR1
RR2
RR3
ST1
SU1
ZD1
ZD2


AGB/ha (t) per inventory year
500
400
300
200
100
AGB/ha (t)
1990
2000
2010
2020
Inventory year
PLOT
BV1
BV2
GO1
ME1
RG1
RG2


AGB/ha (t)
650
600
550
500
450
400
350
300
250
200
150
100
50
1980
1990
2000
2010
2020
Inventory year
Plots
BV1
BV2
DG1
GO1
KR1
KR2
ME1
PE1
PE2
PE3
RG1
RG2
RR1
RR2
RR3
ST1
SU1
ZD1
ZD2

# Primary forest sites to estimate carbon carrying capacity across European forests



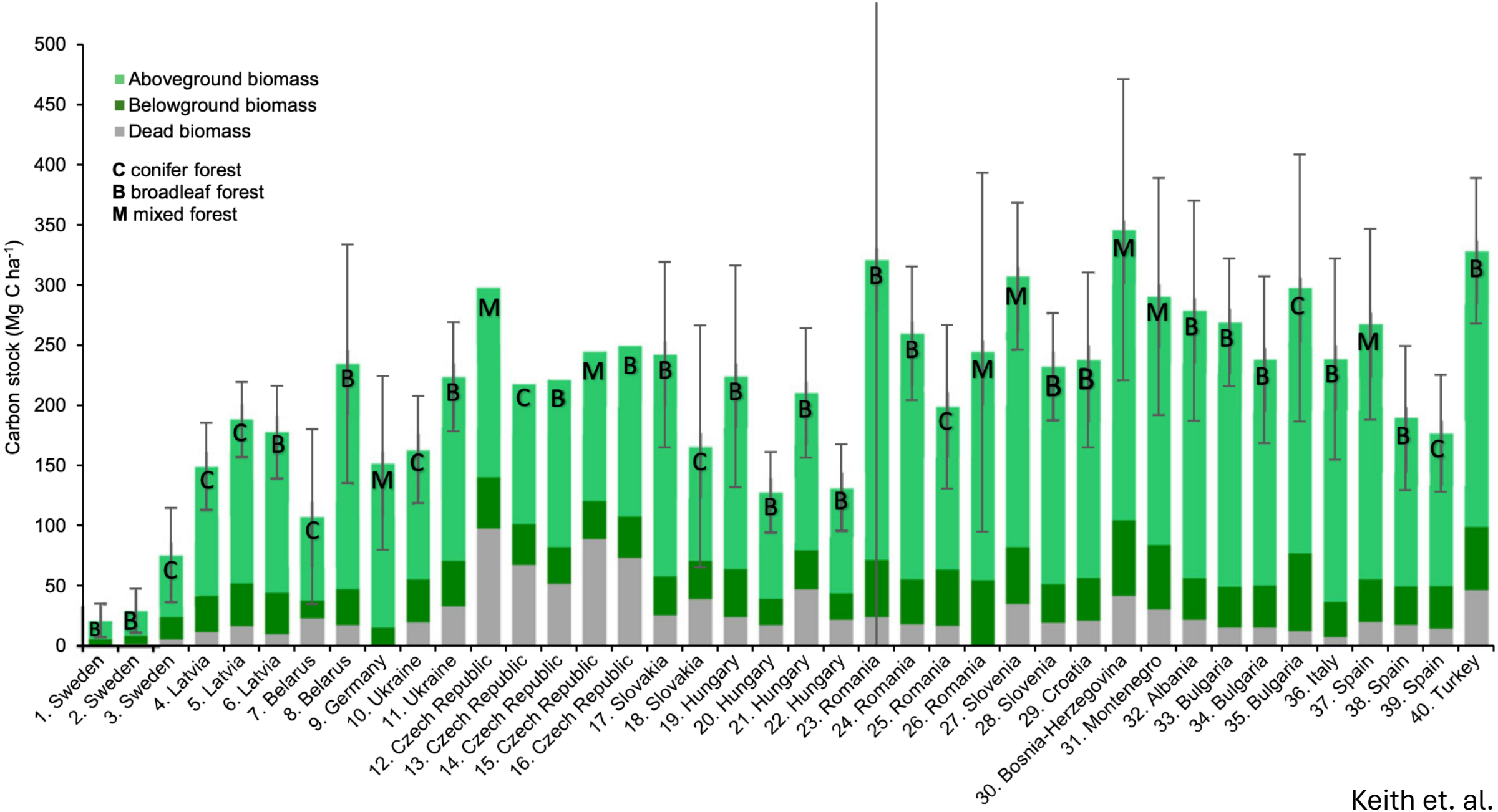

nature › communications earth & environment › articles › article

Article | Open access | Published: 14 May 2024

## Carbon carrying capacity in primary forests shows potential for mitigation achieving the European Green Deal 2030 target

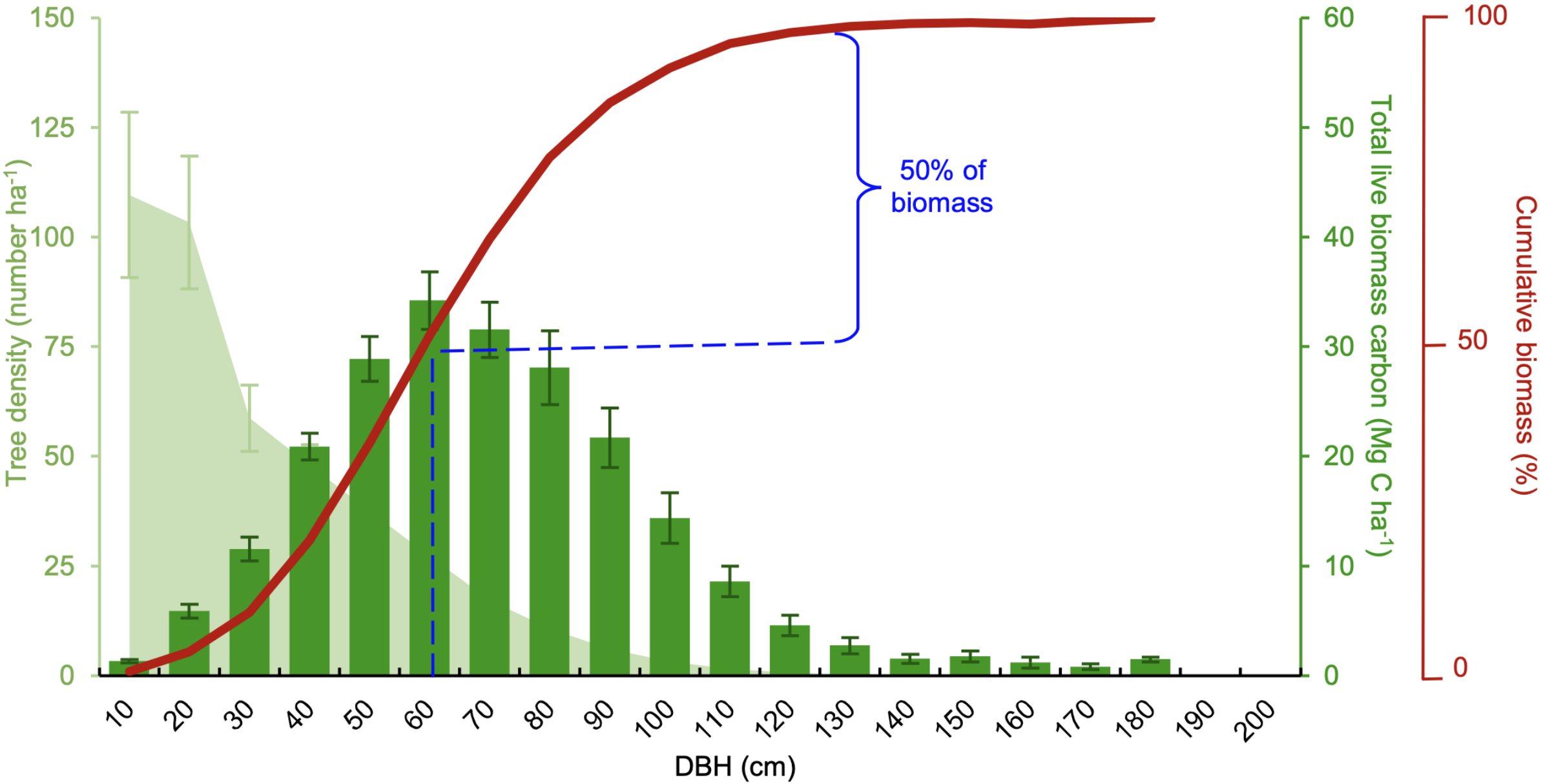
Heather Keith ✉, Zoltàn Kun, Sonia Hugh, Miroslav Svoboda, Martin Mikoláš, Dusan Adam, Dmitry Bernatski, Viorel Blujdea, Friedrich Bohn, Jesús Julio Camarero, László Demeter, Alfredo Di Filippo, Ioan Dutcă, Matteo Garbarino, Ferenc Horváth, Valery Ivkovich, Āris Jansons, Laura Ķēniņa, Kamil Kral, Dario Martin-Benito, Juan Alberto Molina-Valero, Renzo Motta, Thomas A. Nagel, Momchil Panayotov, ... Brendan Mackey + Show authors

*Communications Earth & Environment* **5**, Article number: 256 (2024) | Cite this article

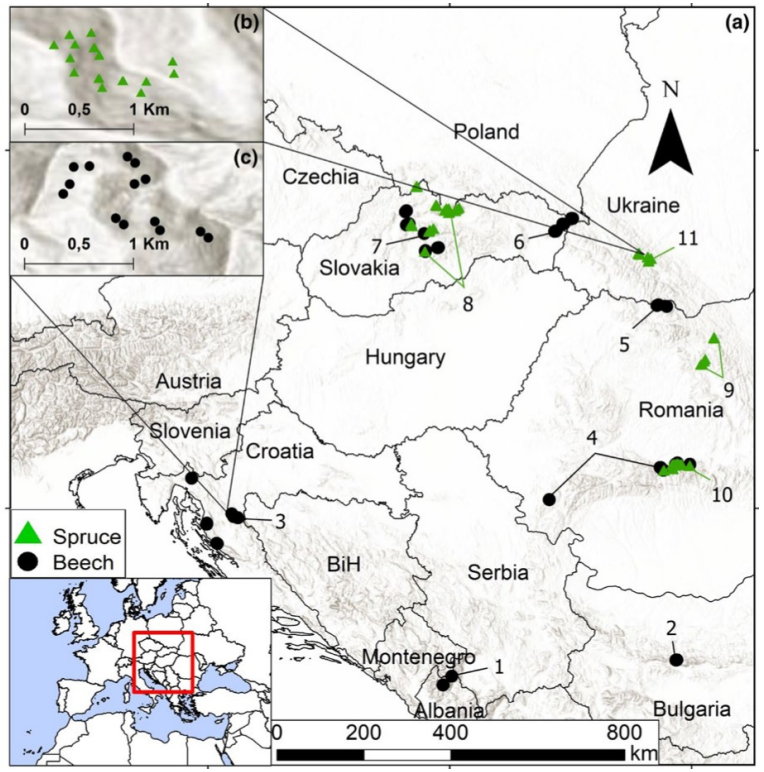

Aboveground biomass
Belowground biomass
Dead biomass
C conifer forest
B broadleaf forest
M mixed forest
Carbon stock (Mg C ha-1)
0
50
100
150
200
250
300
350
400
450
500
1. Sweden
2. Sweden
3. Sweden
4. Latvia
5. Latvia
6. Latvia
7. Belarus
8. Belarus
9. Germany
10. Ukraine
11. Ukraine
12. Czech Republic
13. Czech Republic
14. Czech Republic
15. Czech Republic
16. Czech Republic
17. Slovakia
18. Slovakia
19. Hungary
20. Hungary
21. Hungary
22. Hungary
23. Romania
24. Romania
25. Romania
26. Romania
27. Slovenia
28. Slovenia
29. Croatia
30. Bosnia-Herzegovina
31. Montenegro
32. Albania
33. Bulgaria
34. Bulgaria
35. Bulgaria
36. Italy
37. Spain
38. Spain
39. Spain
40. Turkey

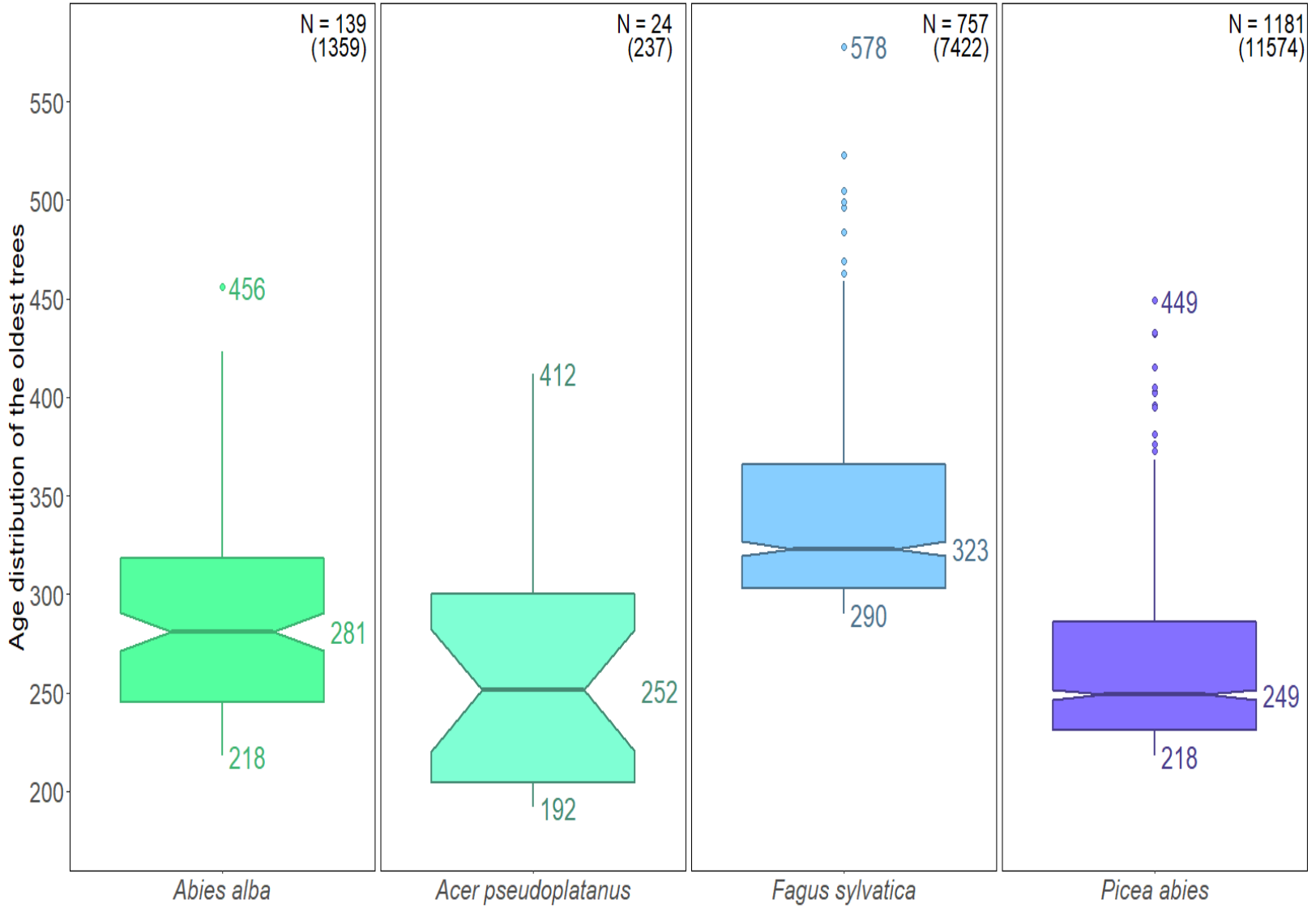
Keith et. al.

Large trees > 60 cm contain 50% of total carbon stock, but only 15% of trees



# Basic biological understanding: tree species differences in longevity




Pavlin et. al. (2021) JVS: https://doi.org/10.1111/jvs.13069

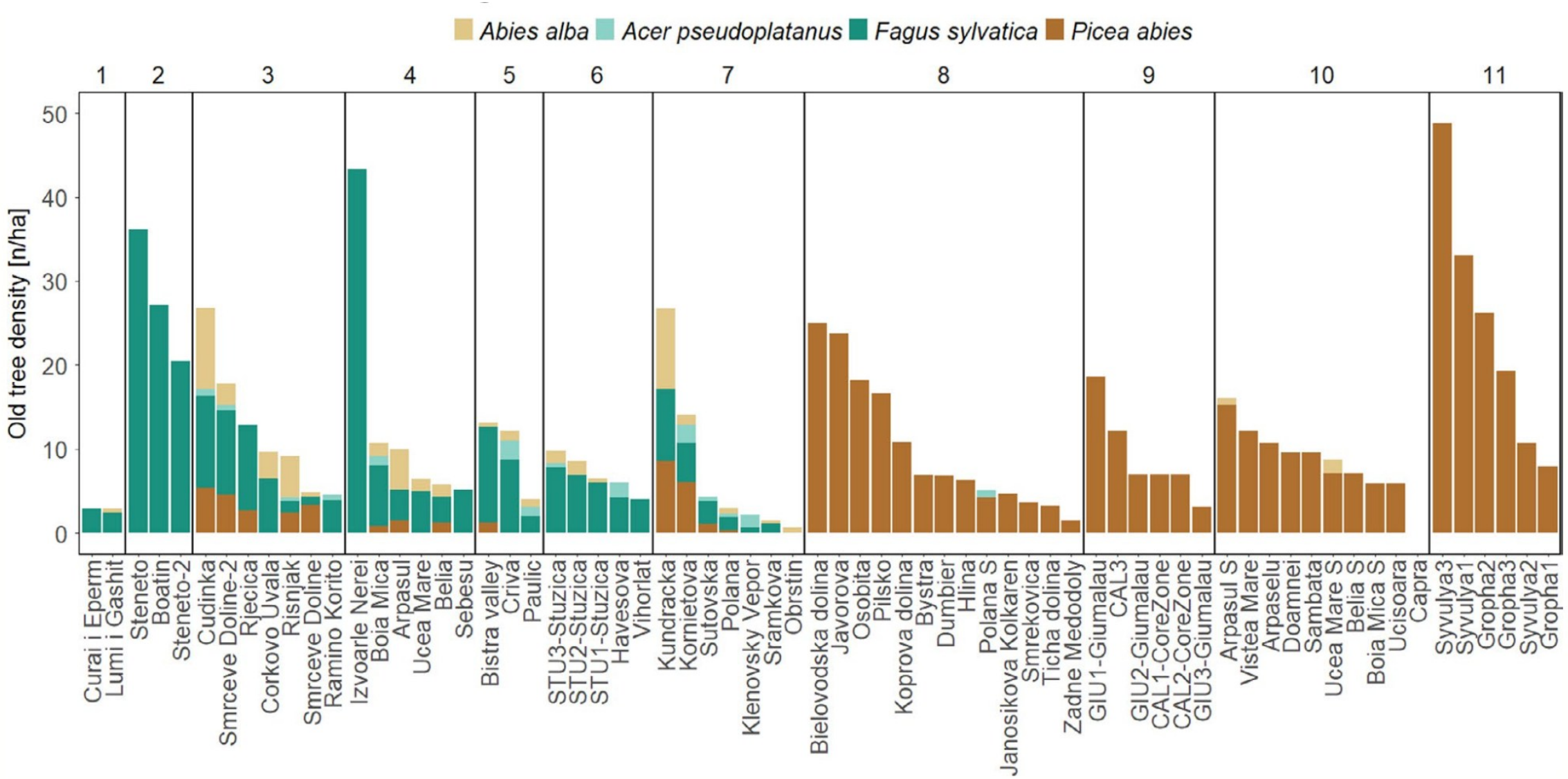



**FIGURE 3** Densities of oldest trees (≥species-specific 90th percentile of age) by species within each stand across the study region. The numbers indicate the forest landscape names: 1, Albania; 2, Bulgaria; 3, Croatia; 4, South Romania beech; 5, North Romania beech; 6, East Slovakia; 7, Central Slovakia beech; 8, Central Slovakia spruce; 9, North Romania spruce; 10, South Romania spruce; 11, Ukraine

# Implications for conservation and policy

# World population to hit 11bn in 2100 – with 70% chance of continuous rise

New study overturns 20 years of consensus on peak projection of 9bn and gradual decline

A crowded Oshodi market in Lagos, Nigeria – the country's population is expected to soar from 200m today to 900m by 2100. Photograph: James Marshall/Corbis

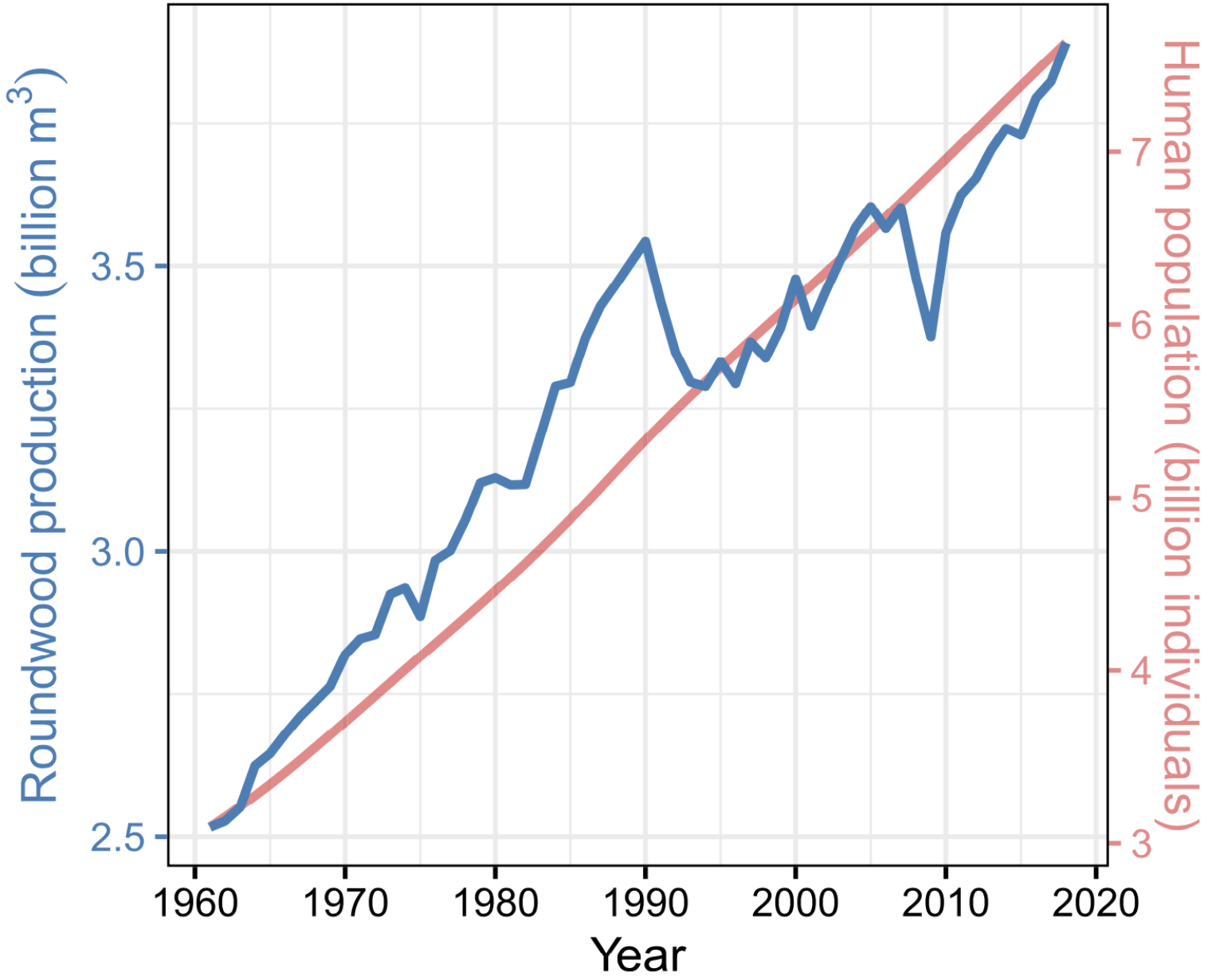
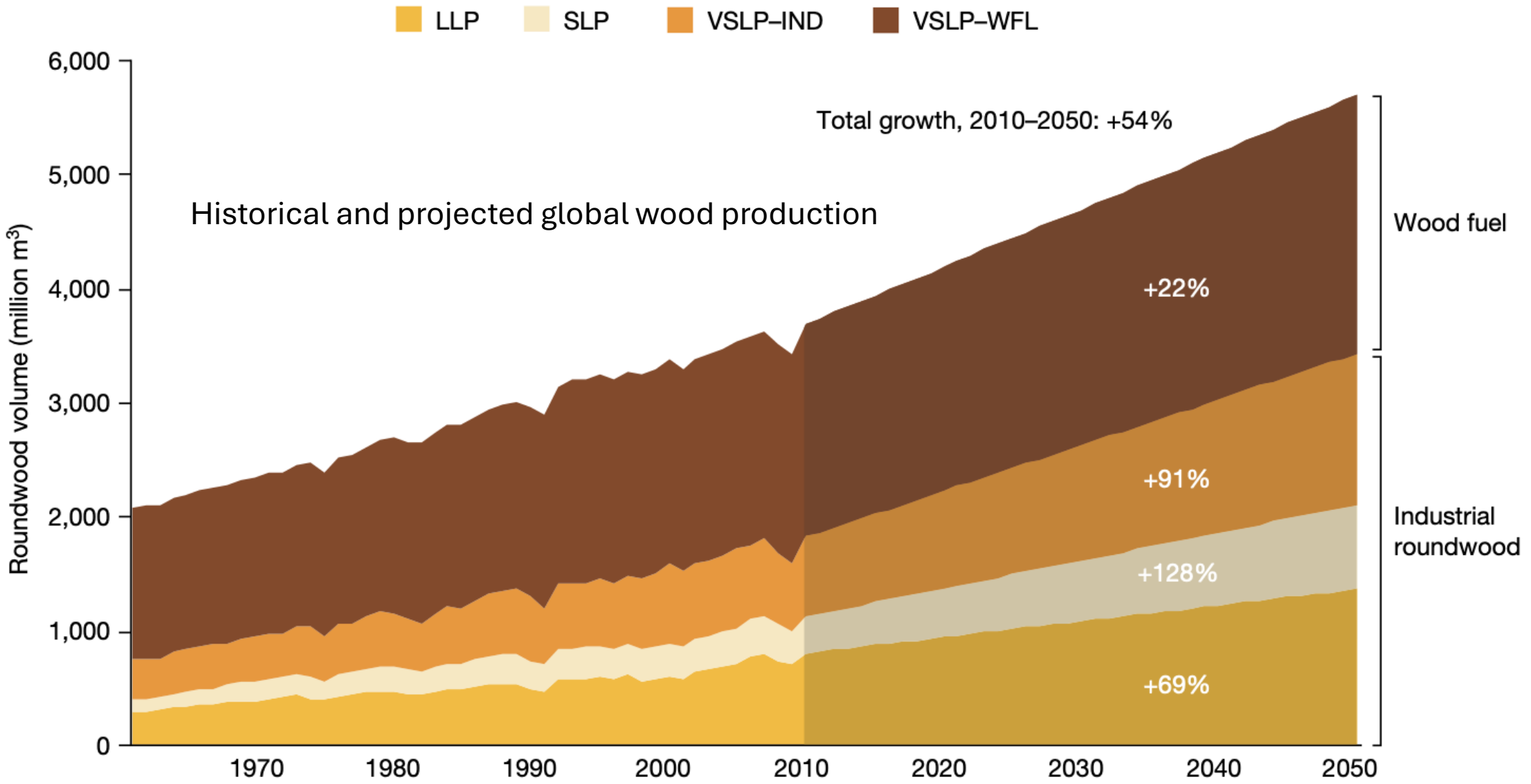



**Fig 1.** Global roundwood production (blue) and human population size (red). Data sources: FAOSTAT (2019*a*,*b*).

# > 50% increase in wood production by 2050!!




Peng et. al. 2023 Nature: https://doi.org/10.1038/s41586-023-06187-1

Increasing demand for forest products
(economic function)

Biodiversity and Ecosystem services (e.g. carbon storage)
(ecological function)

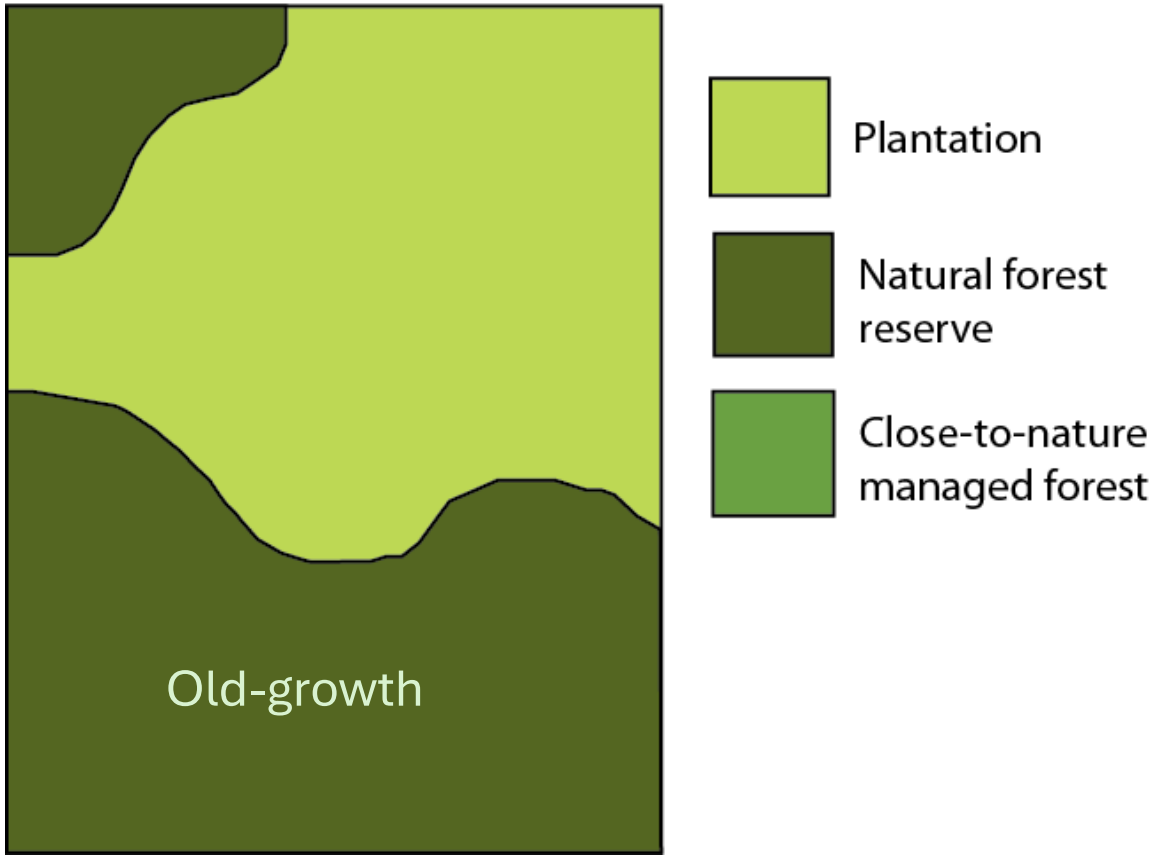
Adaptation to climate change

# Context-EU Biodiversity and Forestry Strategies for 2030, Climate strategy, and Nature Restoration Law

- Call for defining, mapping, monitoring and strictly protecting all remaining primary and old-growth forests
- Strict protection of 10% of land area (most of which should probably be forest)- forest rewilding
- Increased use of integrative “closer to nature” forest management
- High-yield monocultural plantations and clear cutting should be avoided
- Each member state should do its fair share of this protection
- Carbon neutral by 2050, high reliance on forest biomass
- Nature Restoration Law, key element of Biodiversity strategy….each member state creates a plan by 2026…not really clear yet how this will work for forests…. ***“forest ecosystems*** *– achieving an increasing trend for standing and lying deadwood, uneven aged forests, forest connectivity, abundance of common forest birds and stock of organic carbon”*

# How do we produce more timber at least cost to native biodiversity?

## Land sparing
(segregation, intensive)

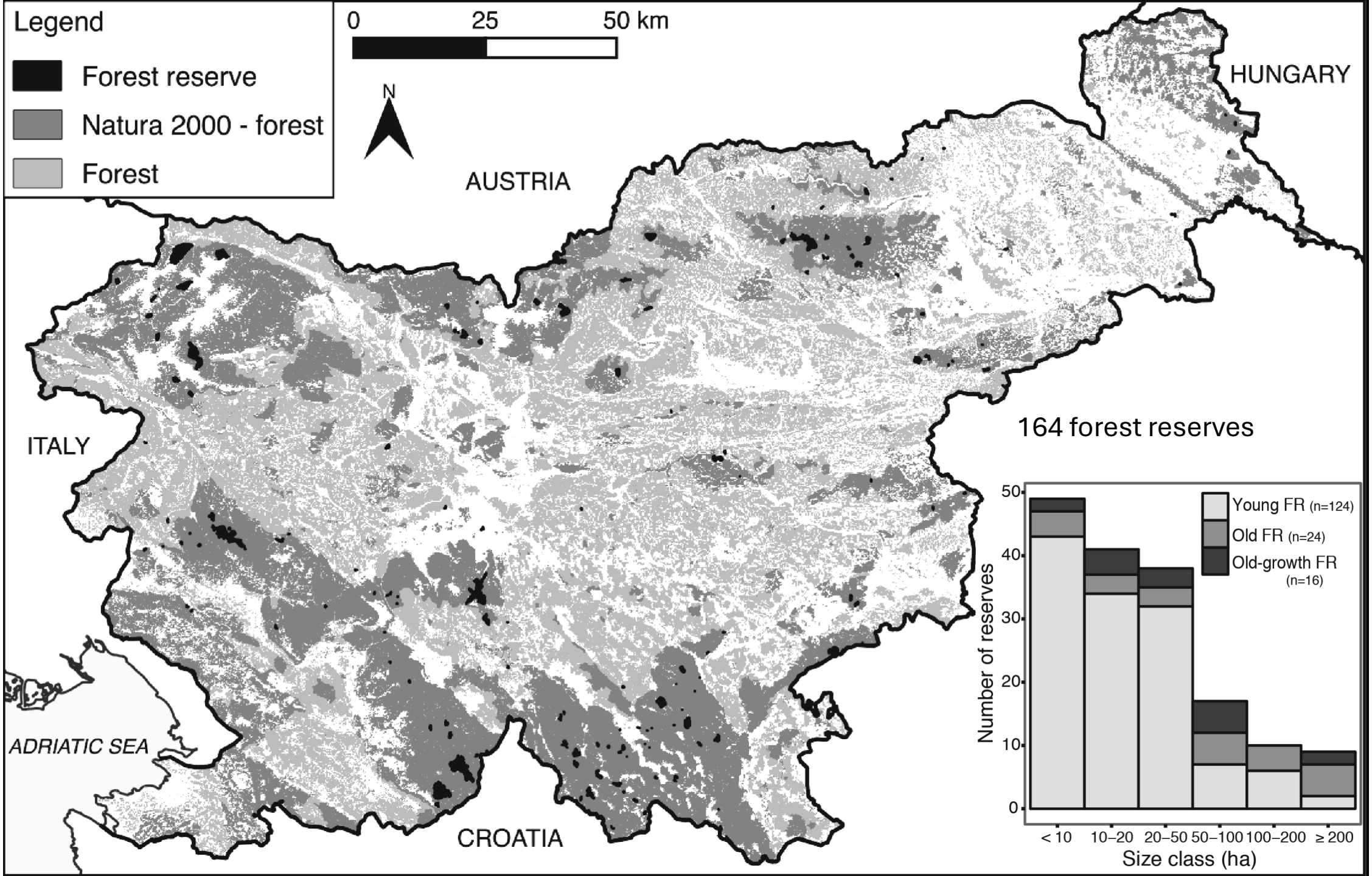


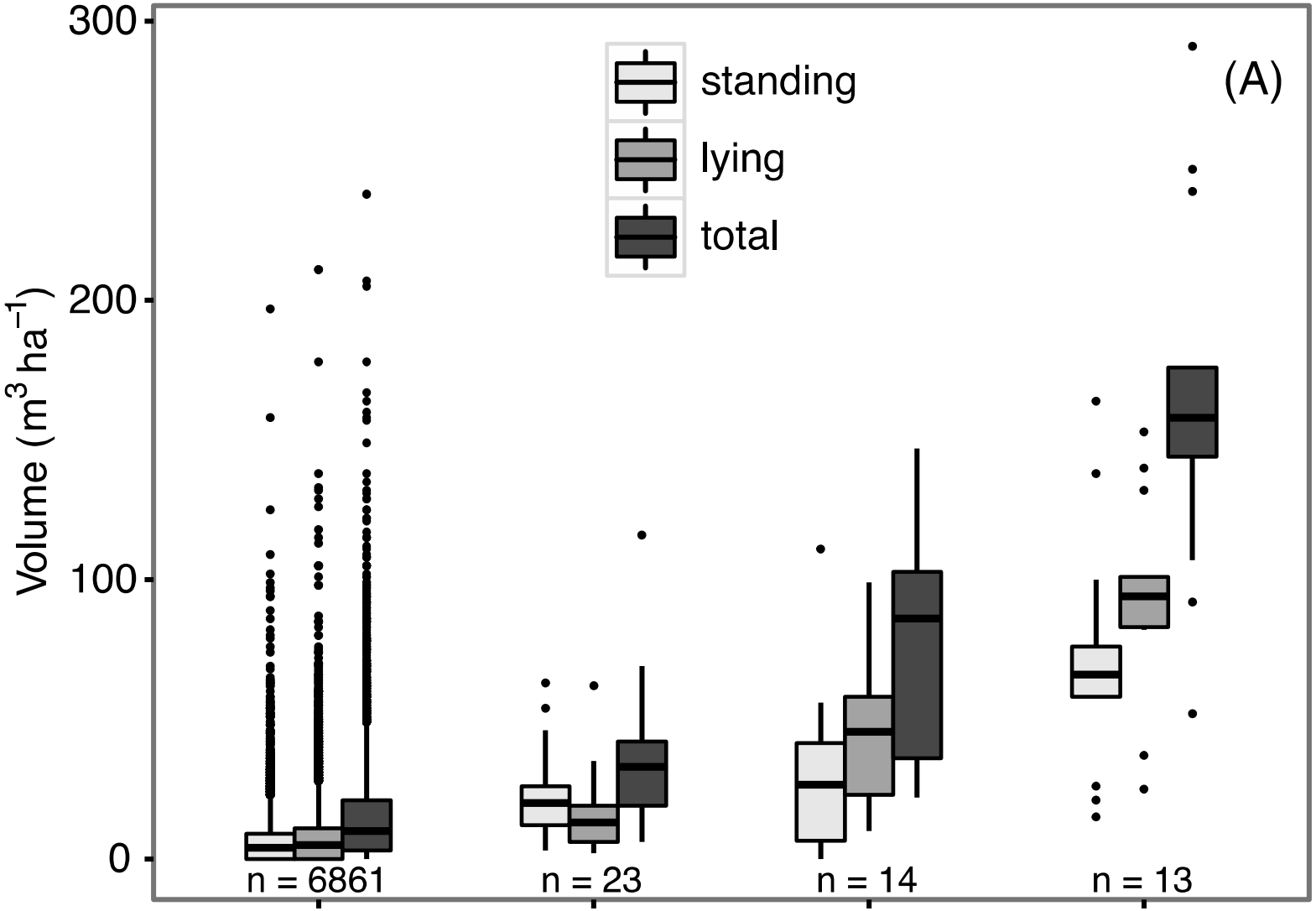

## Land sharing
(integration, extensive)

Simultaneously fulfills wood production and biodiversity conservation

Ecologically based forestry

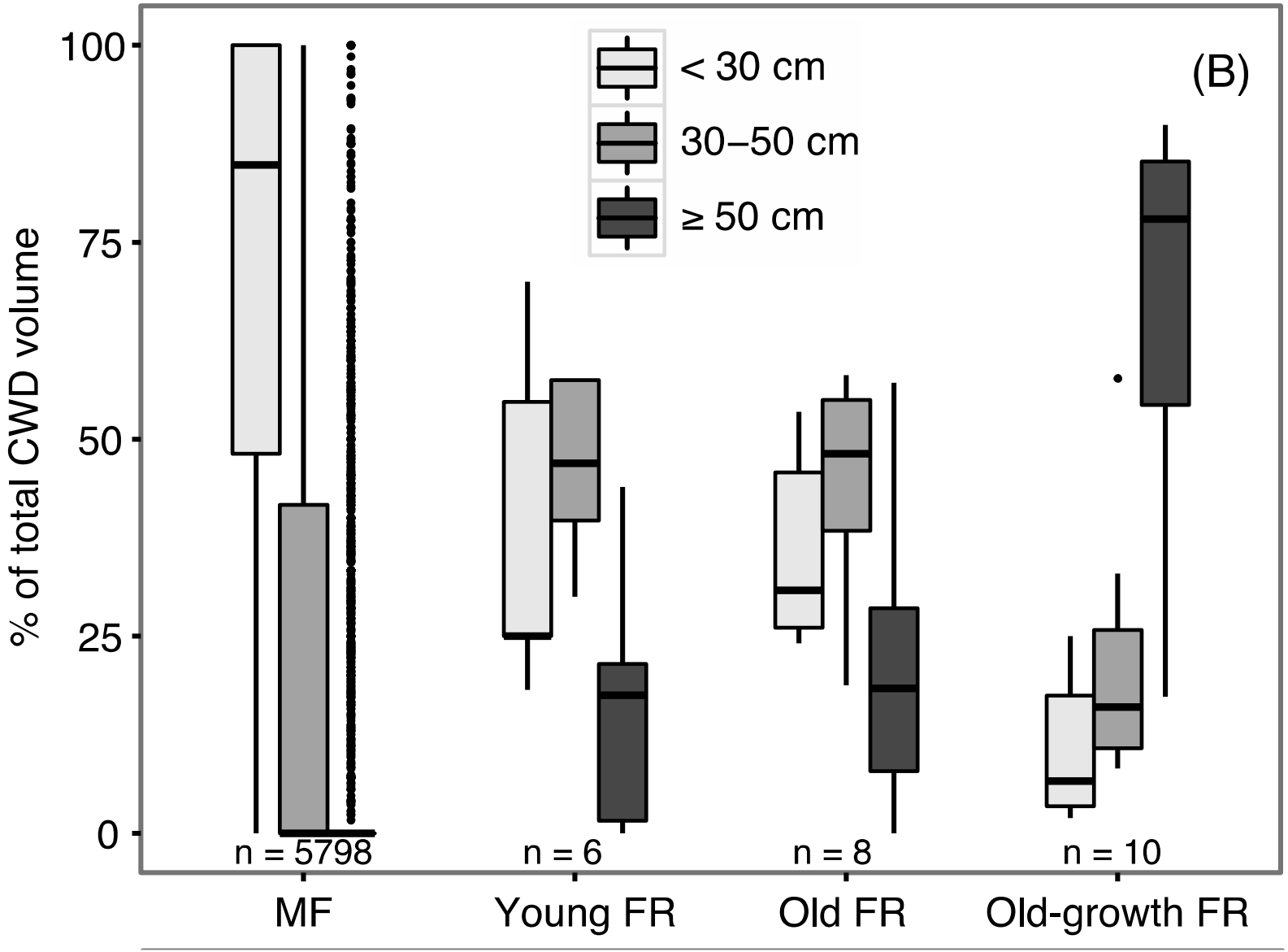
*Presumably* supplants the need for forest reserves

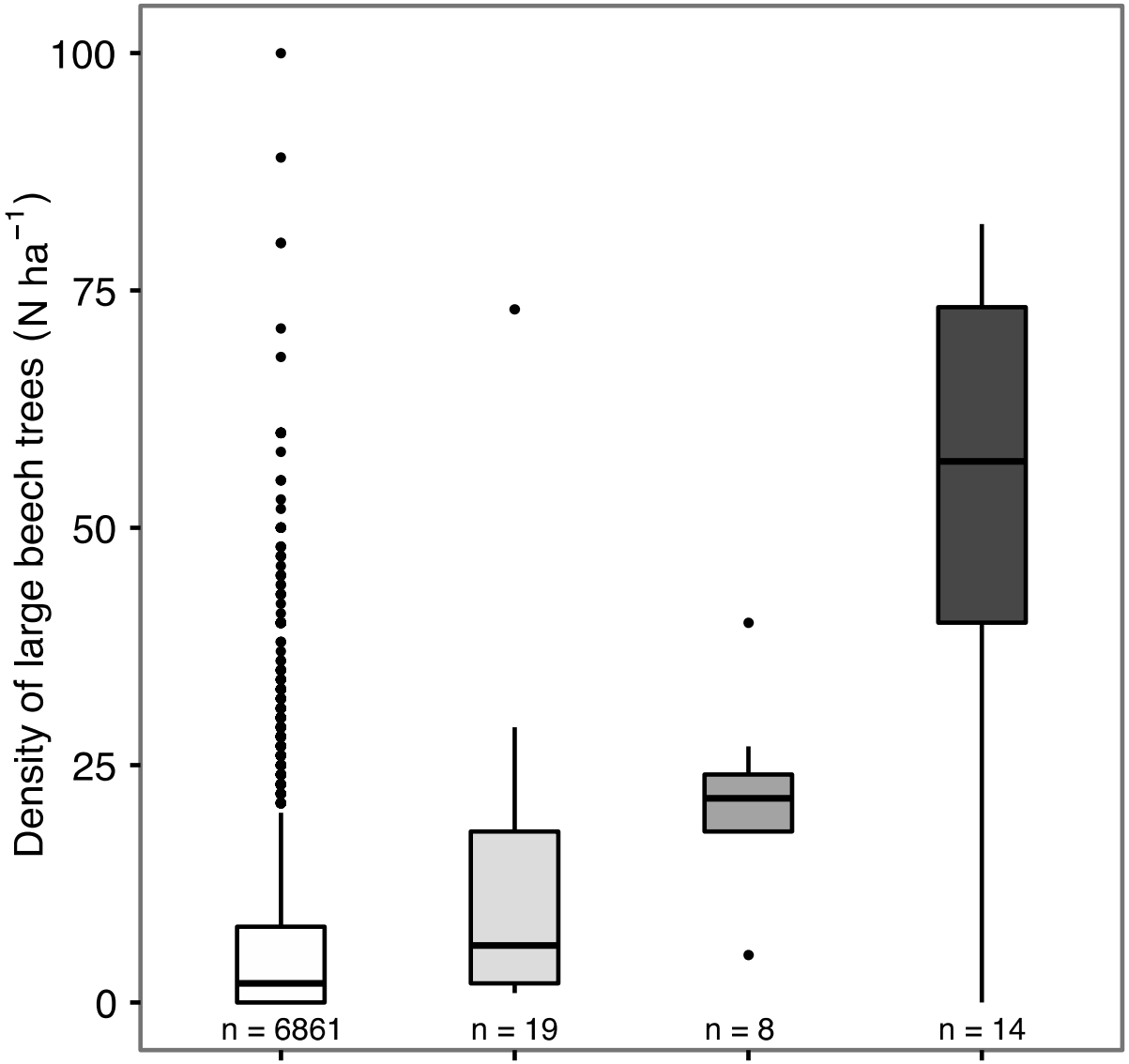

Legend
Forest reserve
Natura 2000 - forest
Forest
0
25
50 km
N
AUSTRIA
HUNGARY
ITALY
ADRIATIC SEA
CROATIA
164 forest reserves
Young FR (n=124)
Old FR (n=24)
Old-growth FR (n=16)
Number of reserves
0
10
20
30
40
50
< 10
10–20
20–50
50–100
100–200
≥ 200
Size class (ha)




| | MF | Young FR | Old FR | Old-growth FR |
|---|---|---|---|---|
| Mean total CWD volume: ($m^3 ha^{-1}$) | 20 | 36 | 76 | 165 |

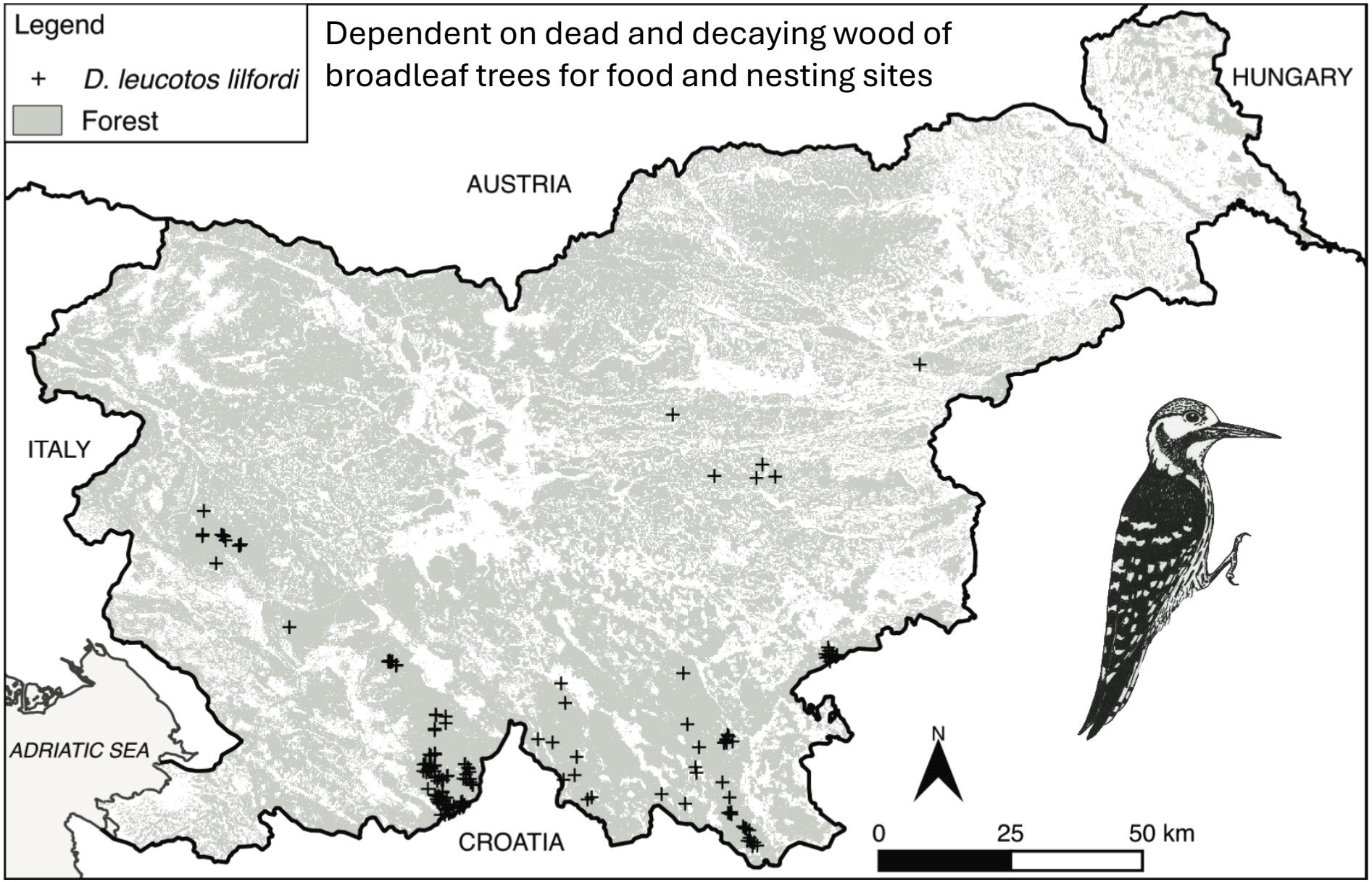
Nagel et al. 2017, Biol Cons. 216: 101-107


(B)
< 30 cm
30–50 cm
≥ 50 cm
% of total CWD volume
100
75
50
25
0
n = 5798
n = 6
n = 8
n = 10
MF
Young FR
Old FR
Old-growth FR

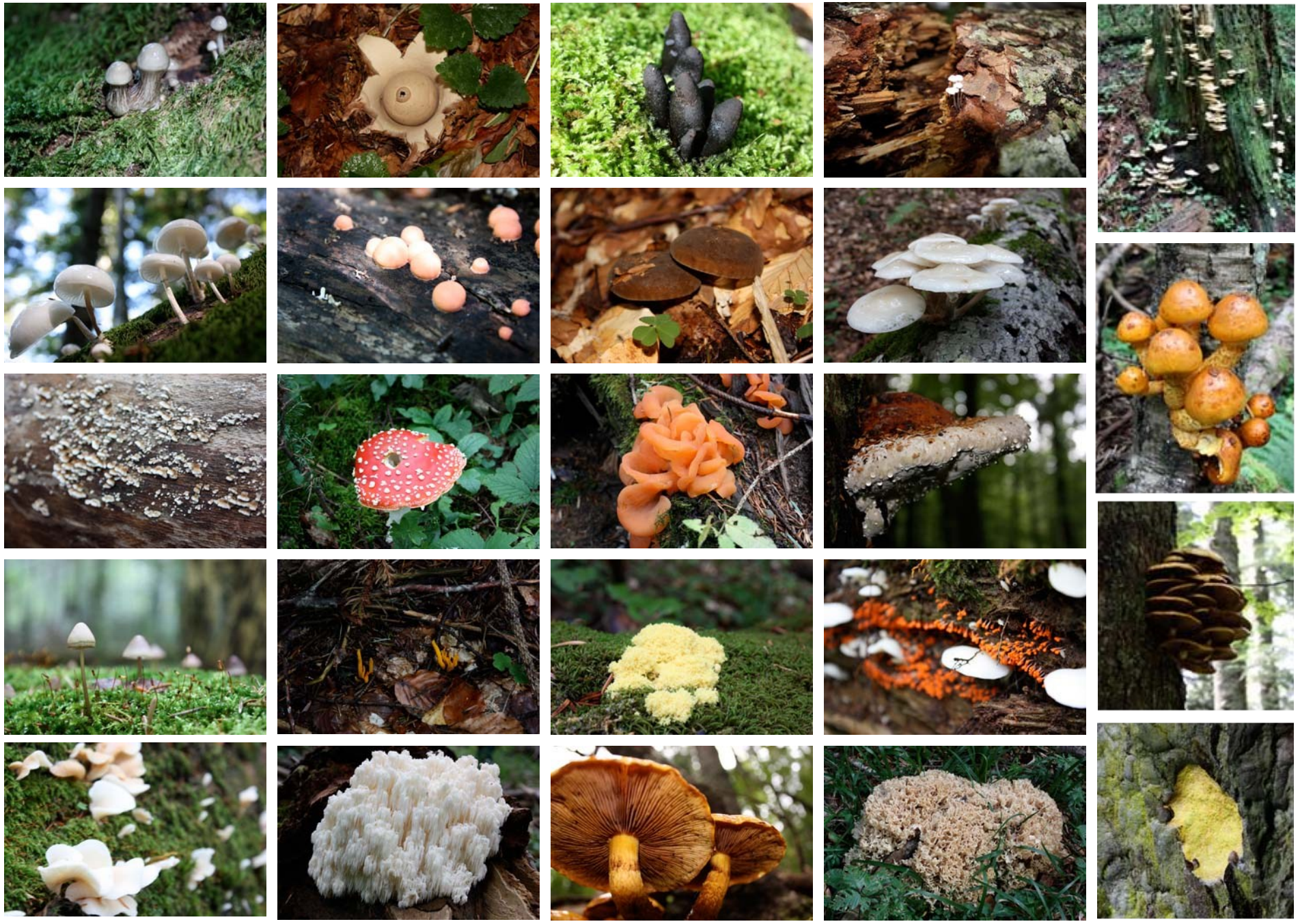



| Mean N ha$^{-1}$ : | 6 | 13 | 22 | 55 |
|---|---|---|---|---|

Distribution of the White-backed woodpecker (*Dendrocopos leucotos lilfordi*)




Estimated population size of 100-150 breeding pairs in Slovenia (Denac and Mihelic, 2015)



Forest Biodiversity, e.g. Fungi on dead wood, Peručica, BiH

# Biodiversity dependent on dead wood is in decline

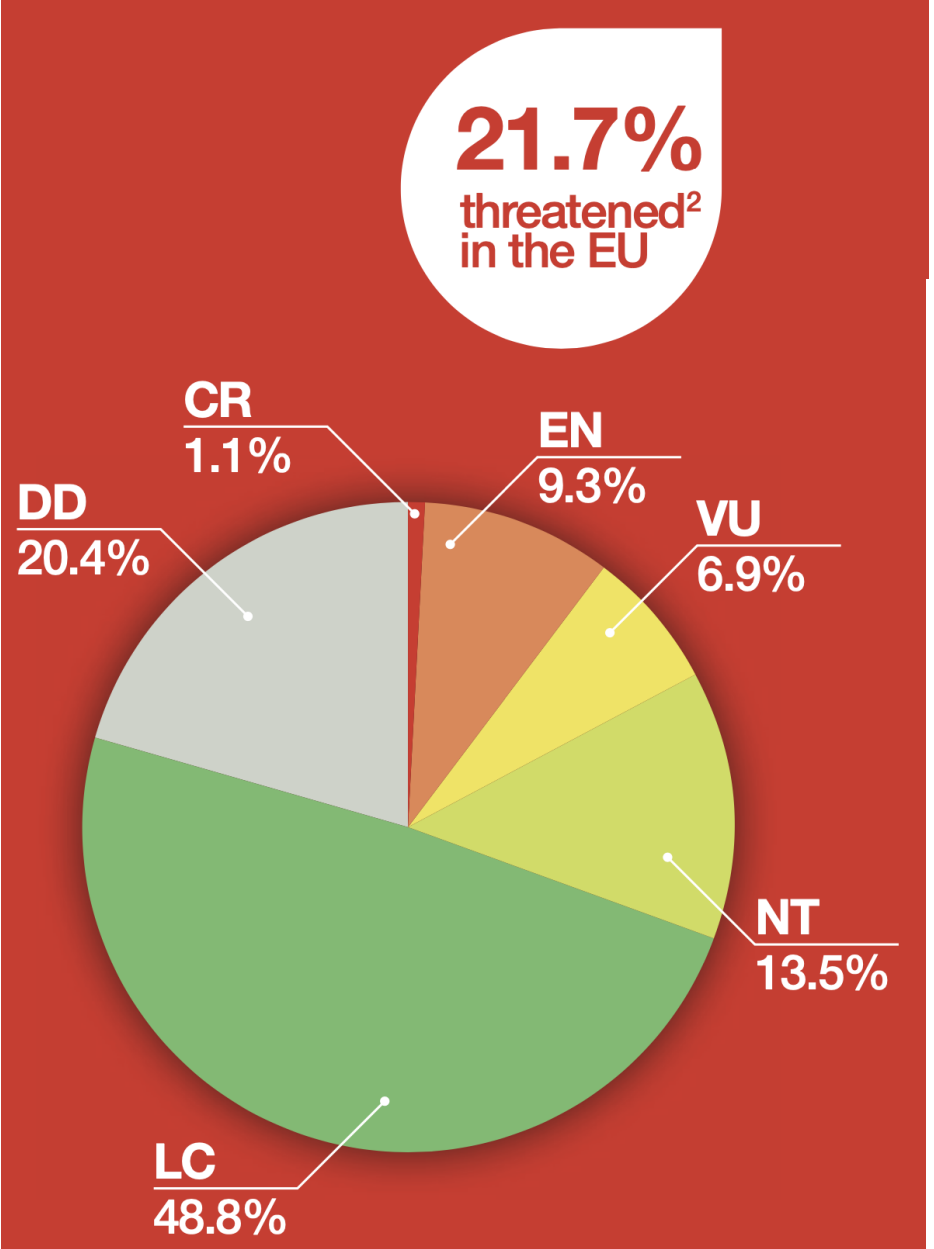
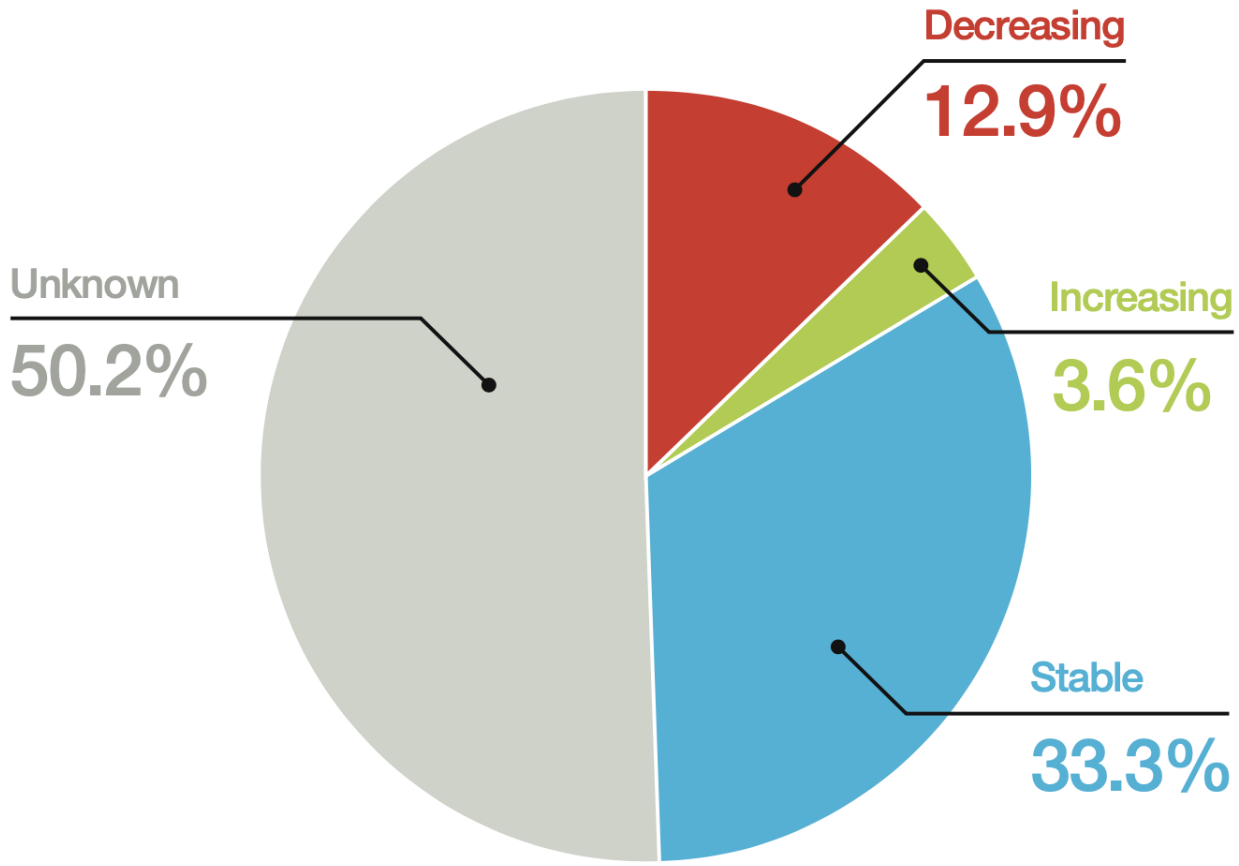


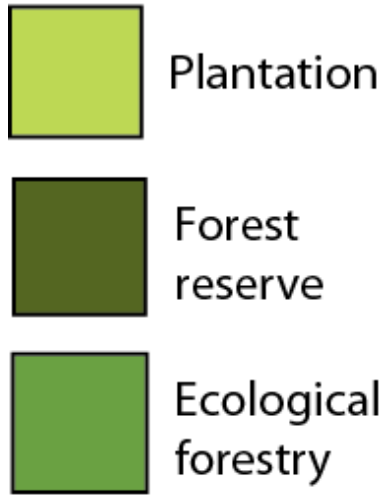

**Figure 2.** IUCN Red List status of saproxylic beetles in the EU.

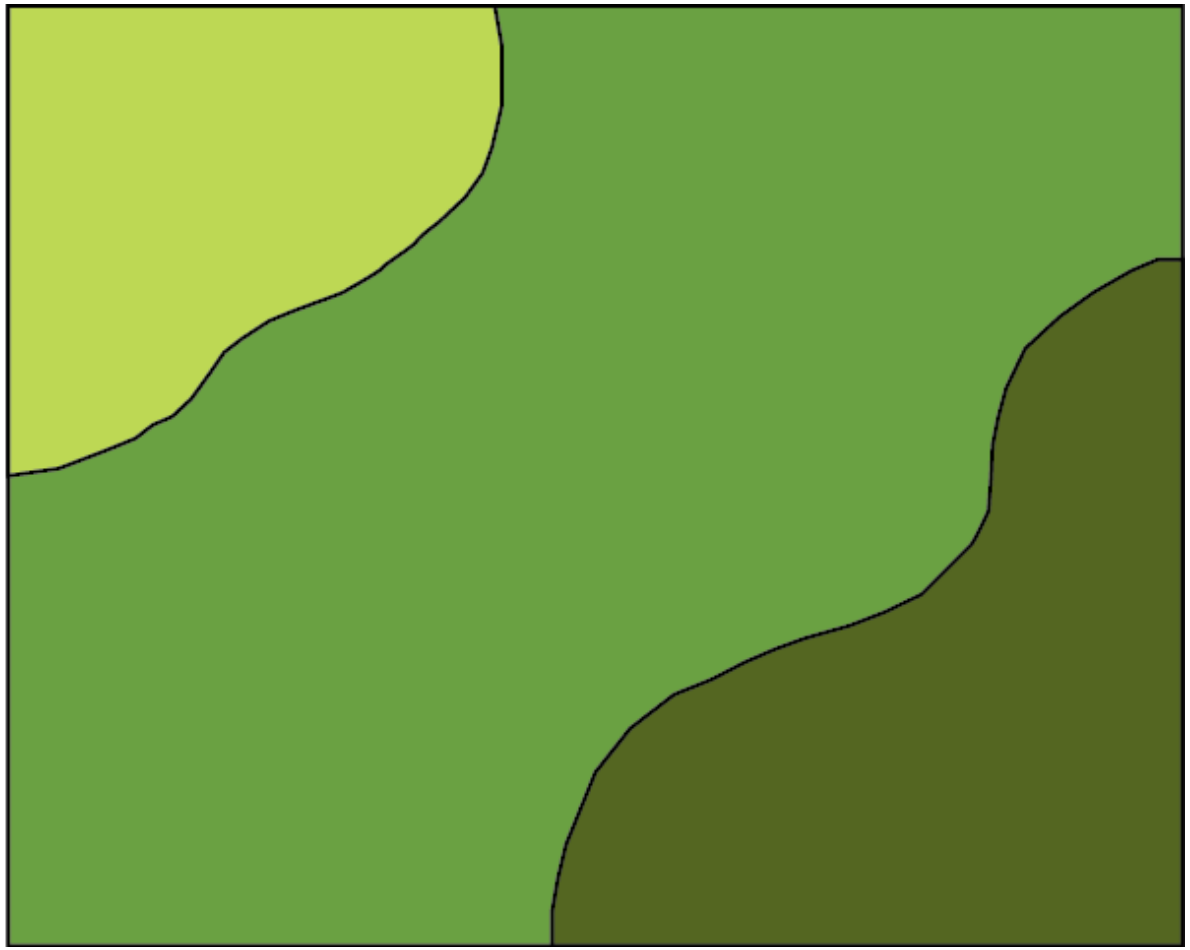
**Figure 4.** Population trends of European saproxylic beetles.

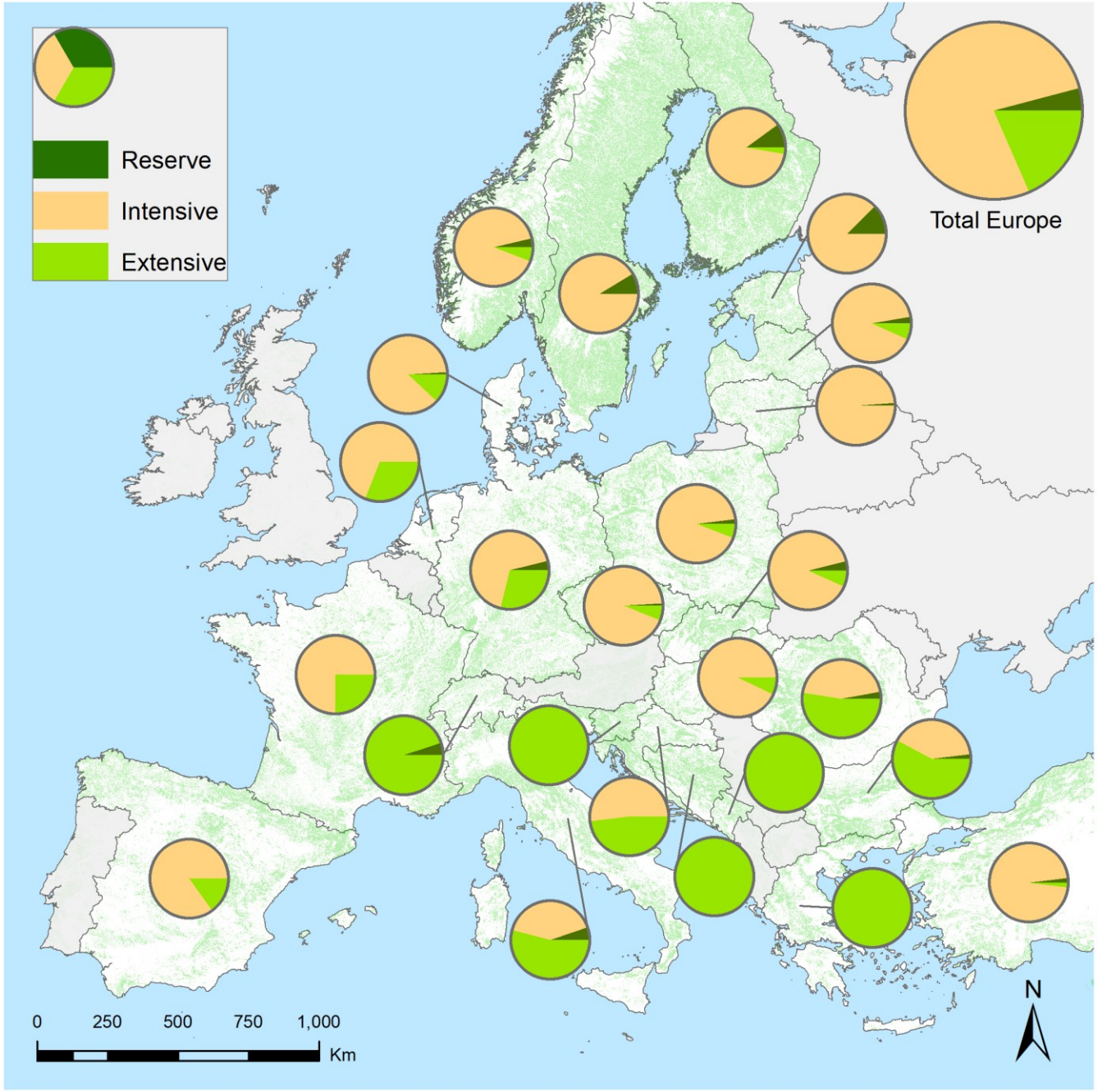


# How can we increase strict forest reserves and wood production?

TRIAD zoning



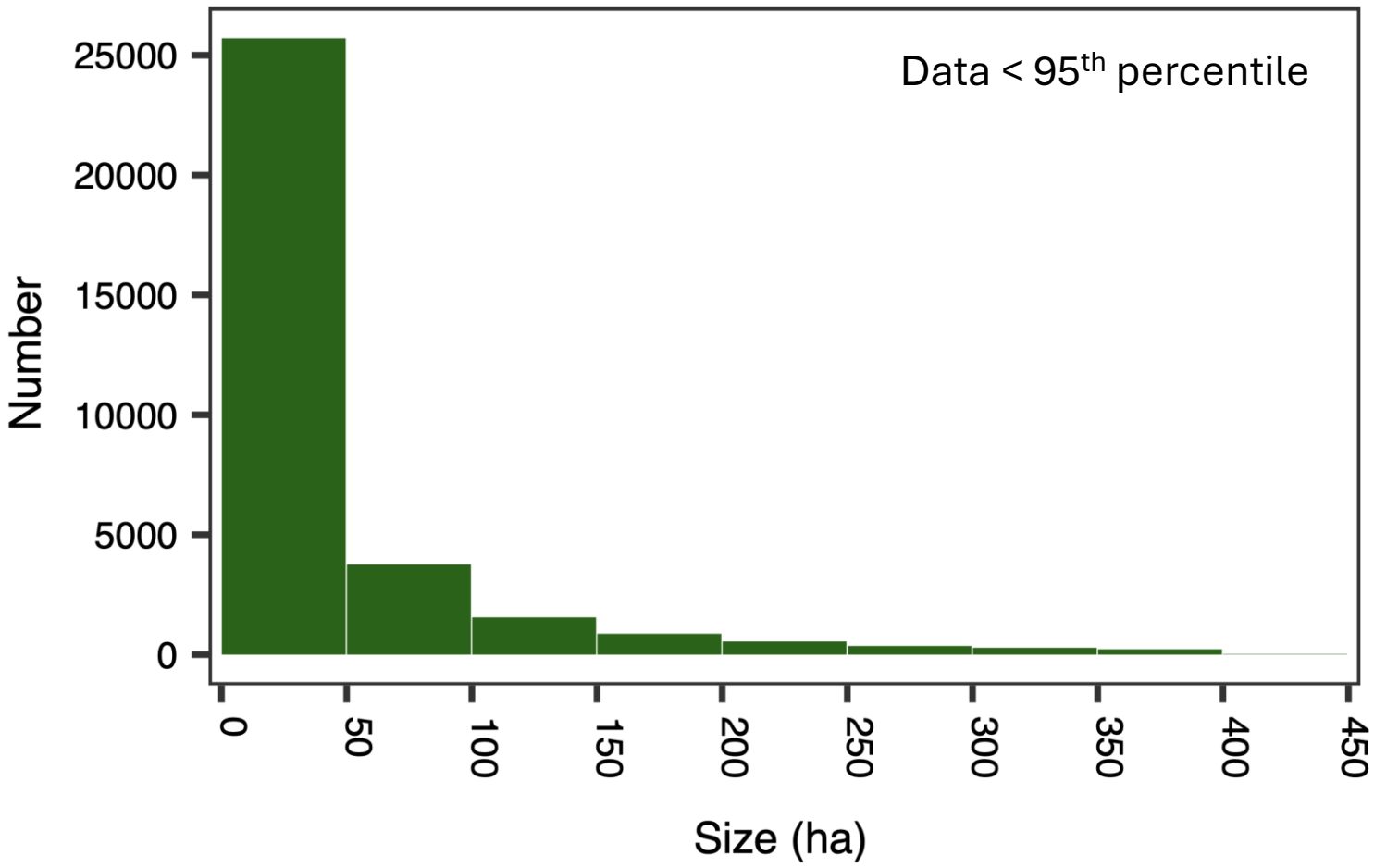






- A few countries have > 10% of forest area strictly protected (e.g. Estonia, Finland), some > 5%
- Most less than 2%
- As a whole, 3.8% (7.2 million ha) of the total forest area in the dataset is under strict protection
- Many countries with less than 1% strictly protected forest area

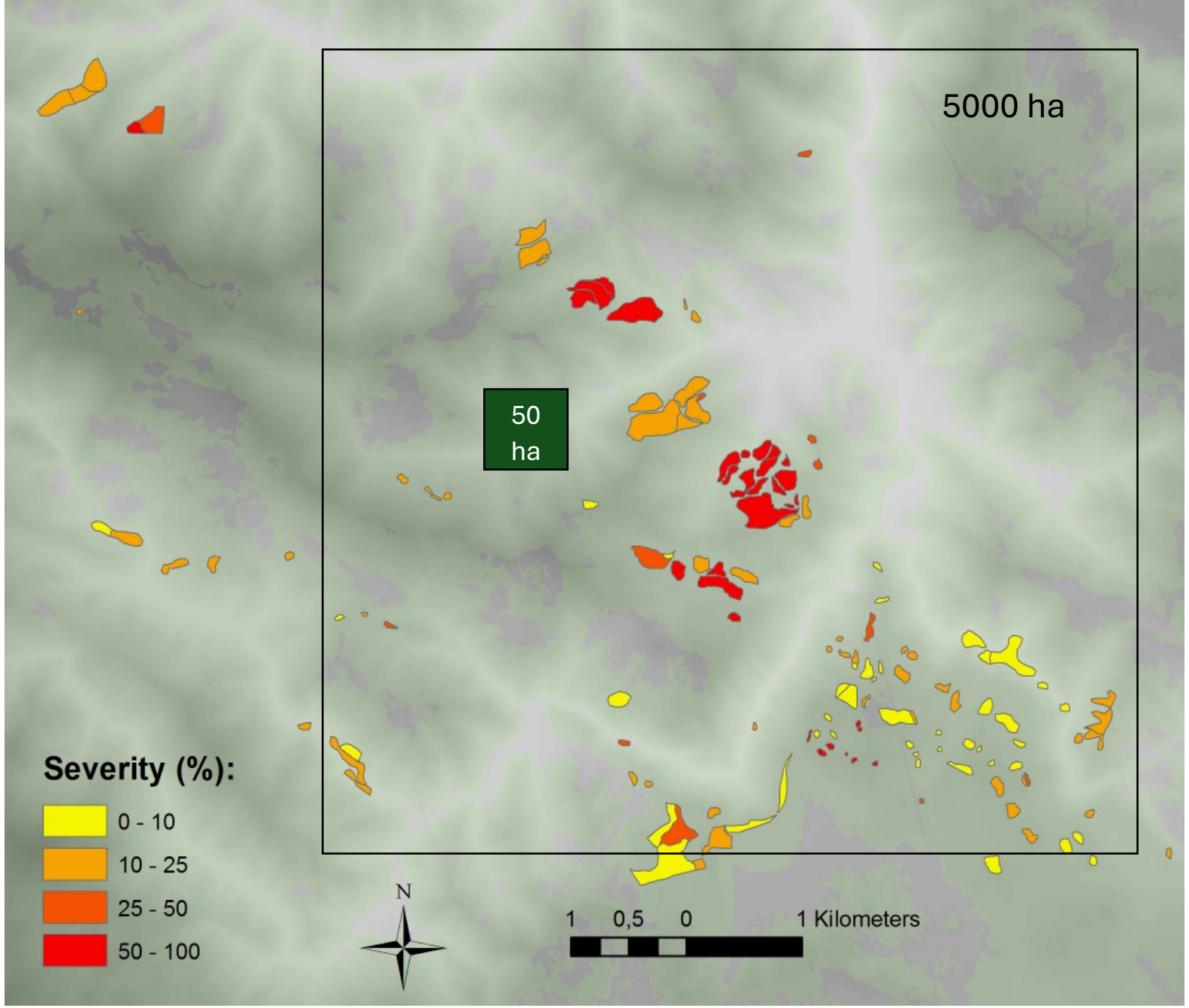
- Italy – 5%

Nagel et. al. Ambio, 2025




- >35,000 strictly protected areas
- 71% < 50 ha in size
- 50% < 20 ha
- Only 2% > 1000 ha
- 44 areas > 10,000, mostly in Sweden, Finland, Turkey
- Too small to capture natural disturbance regimes?

Nagel et. al. Ambio, 2025




Nagel et al. (2017) Forest Ecology and Management

| Step | Latest date |
| --- | --- |
| Member States to submit their pledges to the Commission on protected areas (under NADEG), including on strict protection.<br>In line with the precautionary principle, Member States should without delay strictly protect those forest areas for which there is a strong probability, on the basis of the currently available information, that they meet definitions and criteria set out in this document. | Beginning 2023 |
| Develop an identification and mapping methodology. | End 2023 |
| Finalise the mapping of public primary and old-growth forests. | Mid 2025 |
| Finalise the mapping of private primary and old-growth forests. | End 2025 |
| Strictly protect identified and mapped primary and old-growth forests. | End 2029 |

## 2.3. Definition of an old-growth forest

**Old-growth forest: '**A forest stand or area consisting of native tree species that have developed, predominantly through natural processes, structures and dynamics normally associated with late-seral developmental phases in primary or undisturbed forests of the same type. Signs of former human activities may be visible, but they are gradually disappearing or too limited to significantly disturb natural processes.'

Explanatory notes:

1. This definition includes forest stands that originate not only from natural regeneration, but also from planted or sown native tree species (provided that they meet the rest of the definition).

2. This definition includes forest stands where indigenous peoples engage in traditional forest stewardship activities that otherwise meet the definition.

3. This definition includes forest stands with visible signs of abiotic damages (e.g. storms, snow, droughts and fires) and biotic damage (e.g. from insects and diseases) that meet the definition (see the third additional note in Section 2.4).

4. Forests with visible signs of past human activity are not excluded from the definition of old-growth forests, unless the magnitude of the impact of the activity is such as to prevent the forest stand from counting as old-growth (see Section 3.2).

5. Old-growth forest stands do not include stands for which there is evidence that they are under active productive management. This includes low-intensity silvicultural regimes and coppicing.

6. Some key characteristics of old-growth forest stands are:

    - they contain structural features and dynamics such as natural regeneration, gap dynamics, large and diverse dead wood, structural complexity, and the presence of old trees, or trees reaching senescent stage and tree-related microhabitats.

    - they have acquired these structural features and dynamics through several decades of natural development without significant human intervention.

# 3.2. Indicators for old-growth forests

All the main indicators and at least two complementary indicators need to be met.

## Main indicators

**1.** Native species

Old-growth forests are composed of native species. However, the presence of a small number of non-native trees should not disqualify a forest from being designated as old-growth, if they do not significantly disturb ecological processes.

**2.** Deadwood

Old-growth forests are characterised by a high proportion and diversity of standing and lying deadwood. The amount and type of deadwood can vary greatly between old-growth forests (depending on the forest type, the local environmental conditions, and the area's recent disturbance history).

**3.** Old or large trees

Old-growth forests are often characterised by a high volume of standing trees relative to earlier development stages for the given forest type and local growing conditions, and by the presence of old or large trees, some of which may reach the maximum age known for the species under the local site conditions.

## Complementary indicators

**4.** Stand origin

Most old-growth forest stands originate from natural regeneration, but some sown or planted forests can meet the definition, if given enough time to develop the characteristics of old growth forests.

**5.** Structural complexity

Old-growth forests are generally characterised by structural complexity. This can include a multi-layer canopy structure, horizontal structural diversity, and soil microrelief structures such as mounds caused by uprooting.

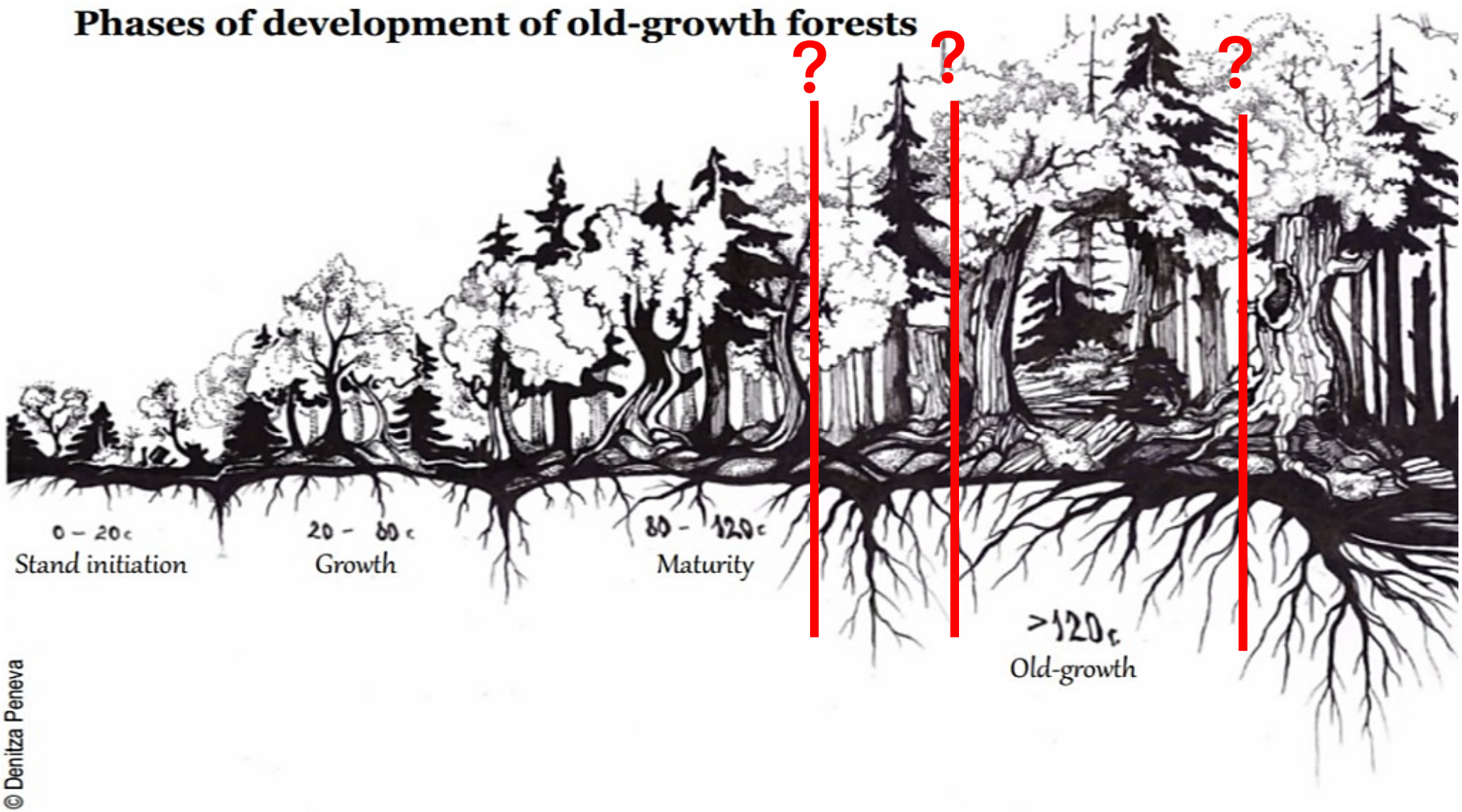
**6.** Habitat trees

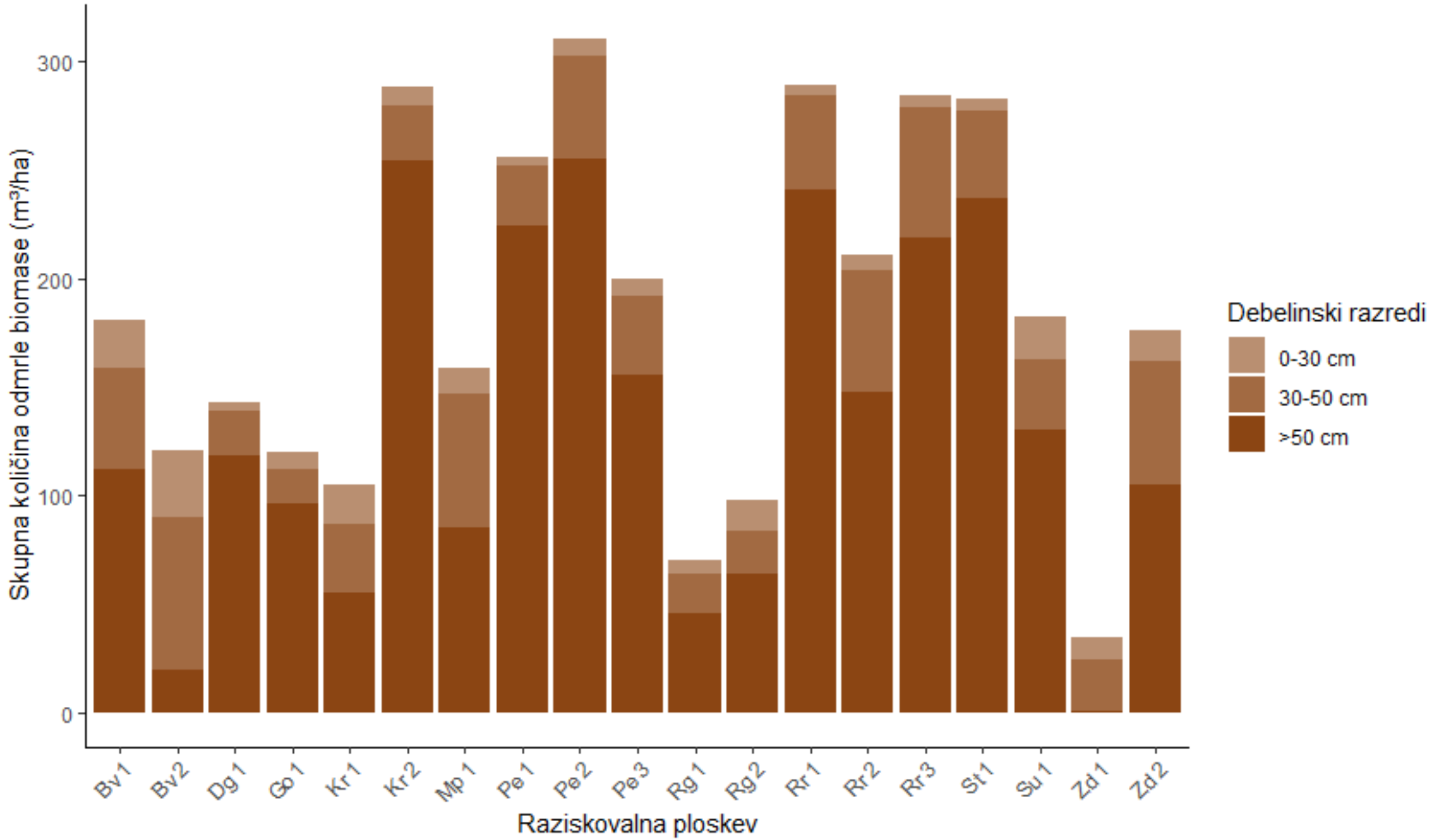
Old-growth forests are often characterised by the high density and high diversity of tree-related microhabitats. These are defined as a 'distinct, well-delineated structure occurring on living or standing dead trees, that constitutes a particular and essential substrate or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed'[14].

**7.** Indicator species

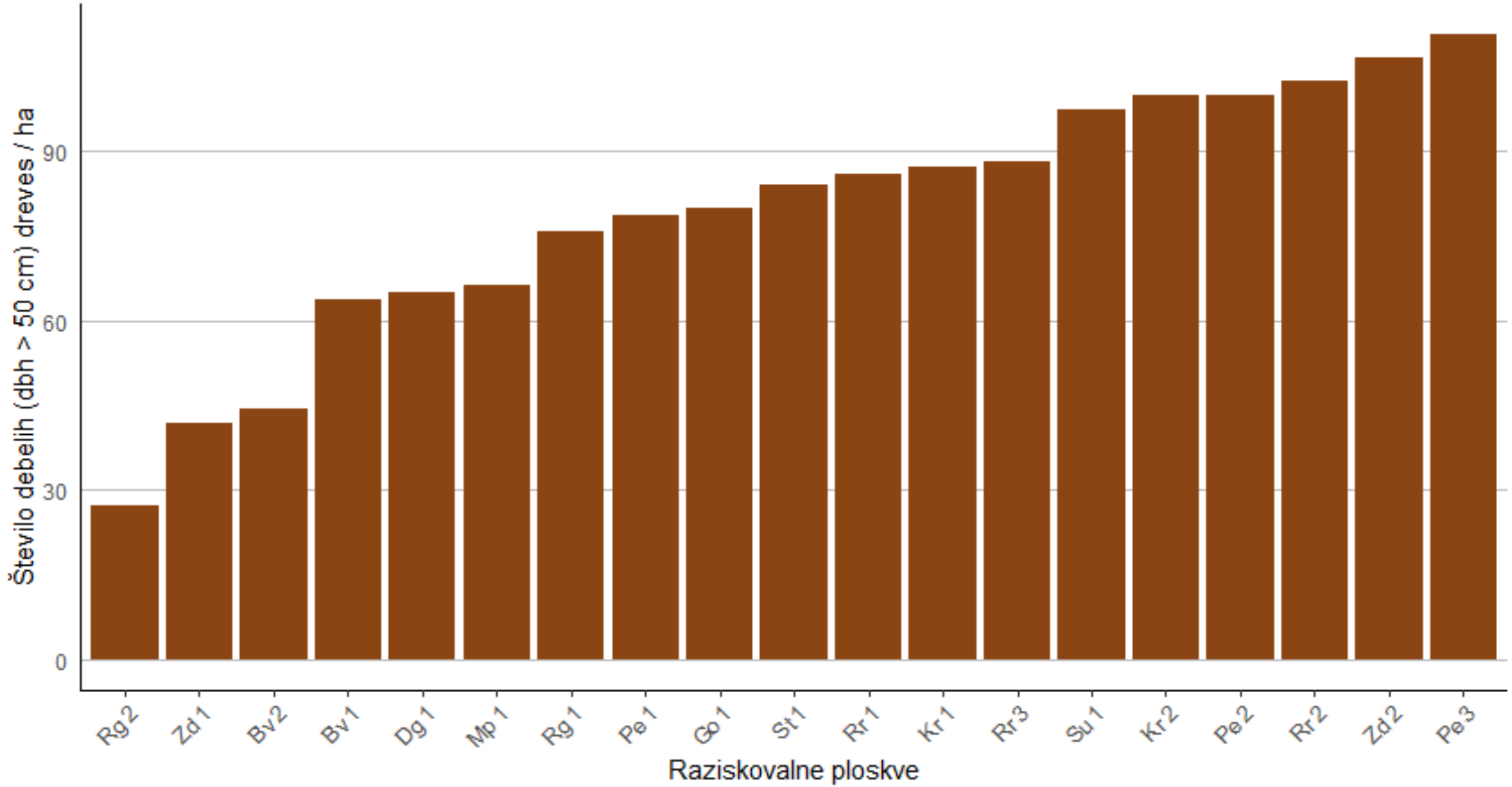
Old-growth forests often host species of late-seral developmental phases that are specific to a certain forest type. These can include species on the red-list of the International Union for Conservation of Nature (IUCN).

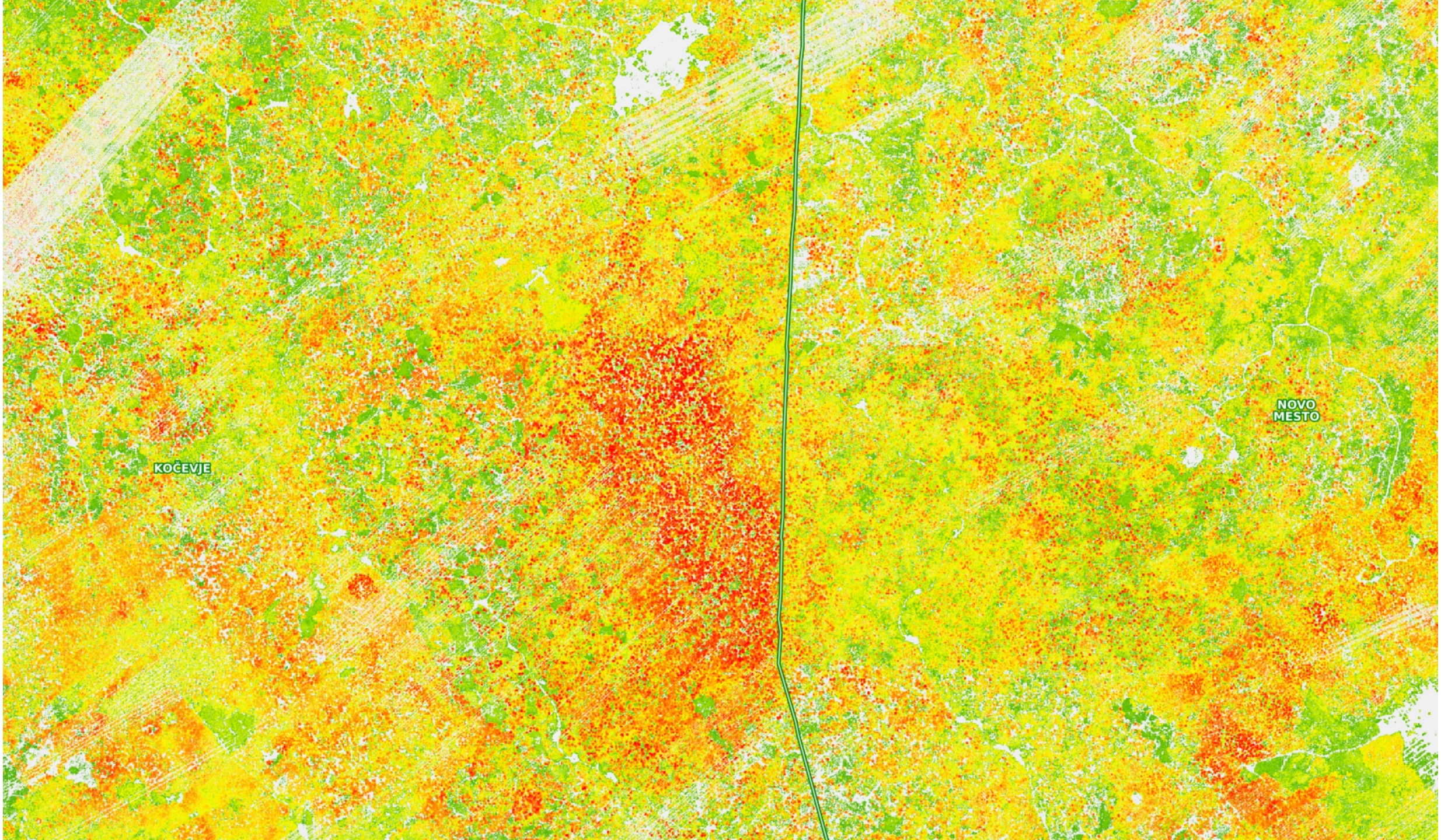
# Level of ‘old-growthness’

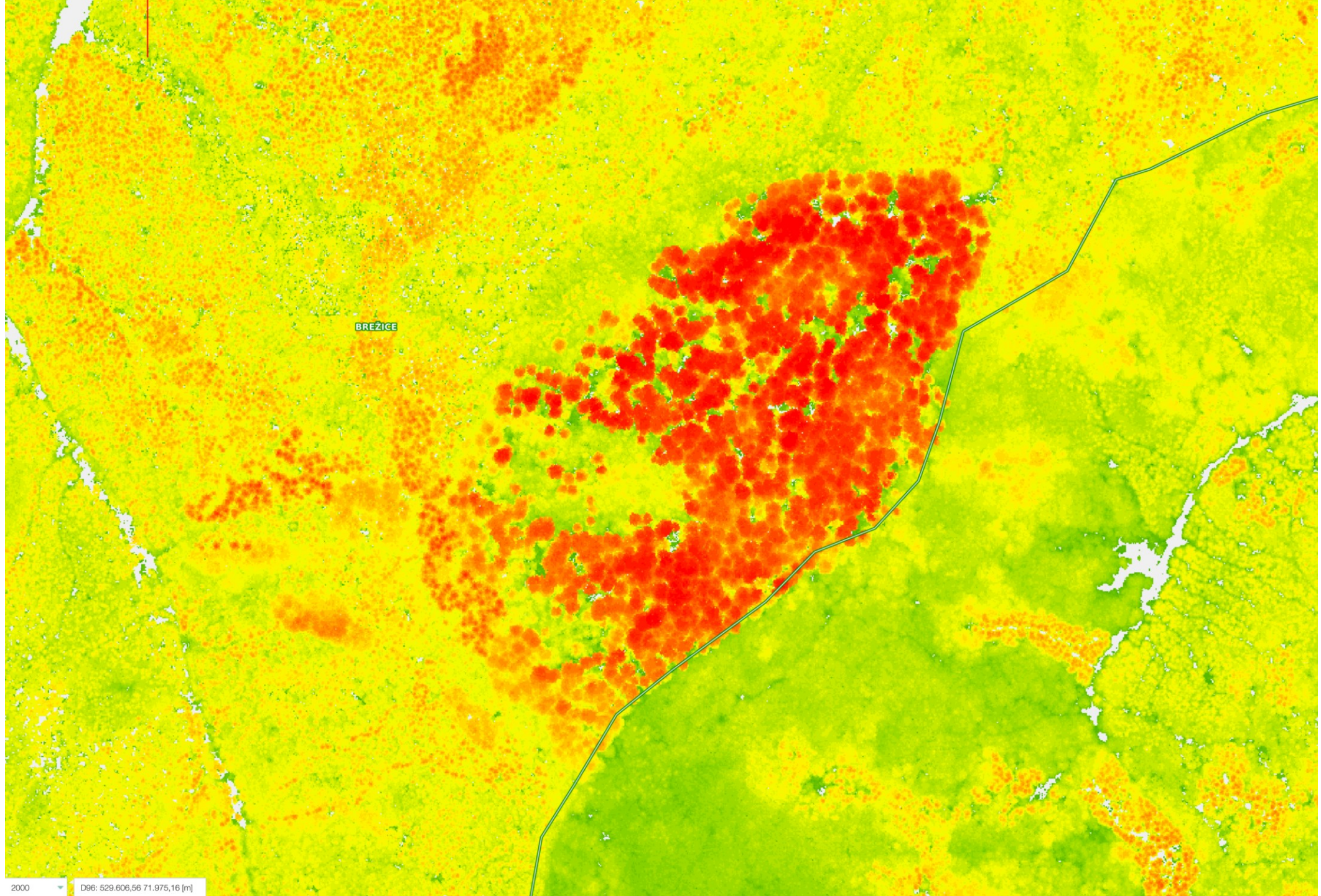


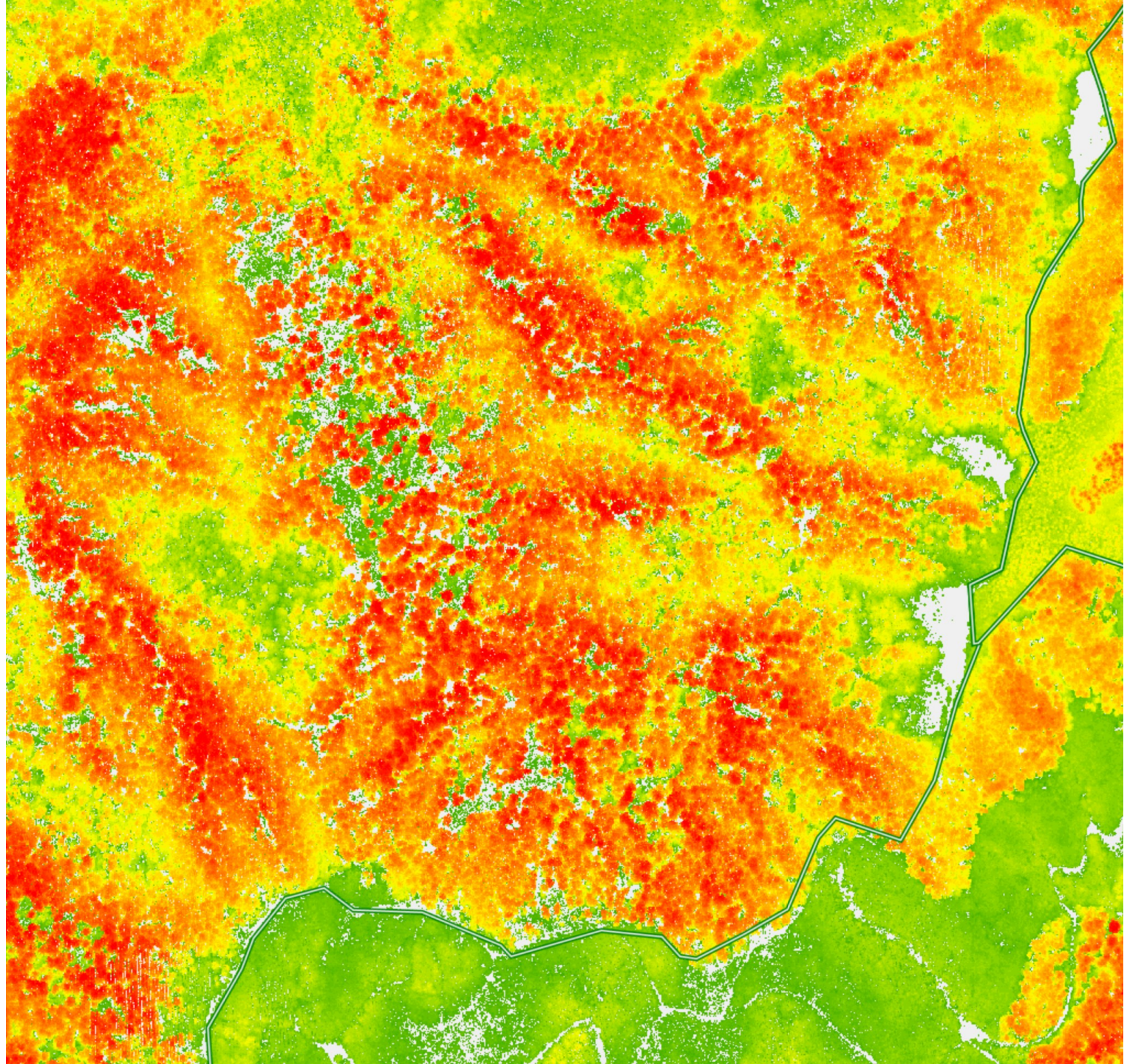

Skupna količina odmrle biomase (m³/ha)
300
200
100
0
Bv1
Bv2
Dg1
Go1
Kr1
Kr2
Mp1
Pe1
Pe2
Pe3
Rg1
Rg2
Rr1
Rr2
Rr3
St1
Su1
Zd1
Zd2
Raziskovalna ploskev
Debelinski razredi
0-30 cm
30-50 cm
>50 cm

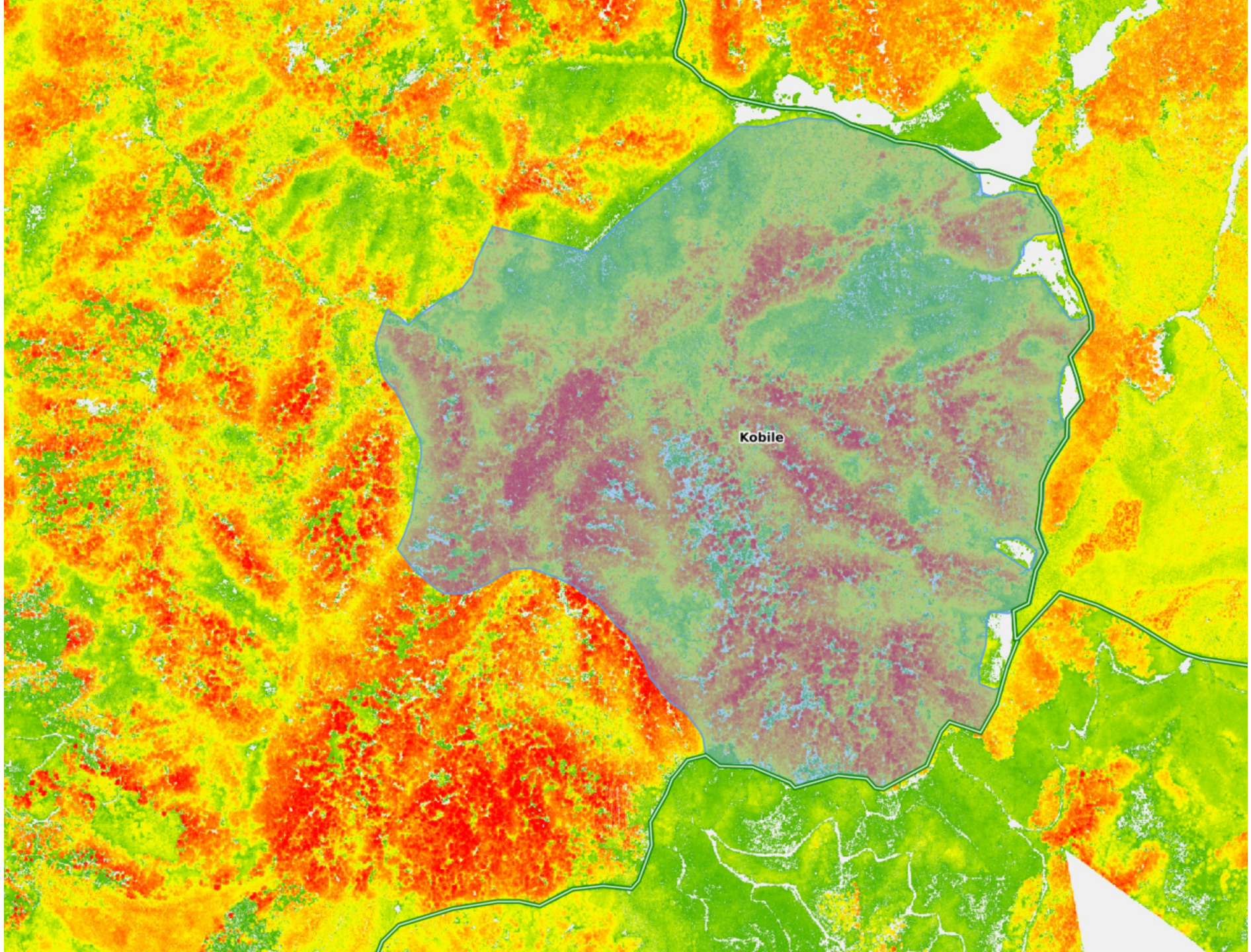
# Density of large trees across old growth plot network

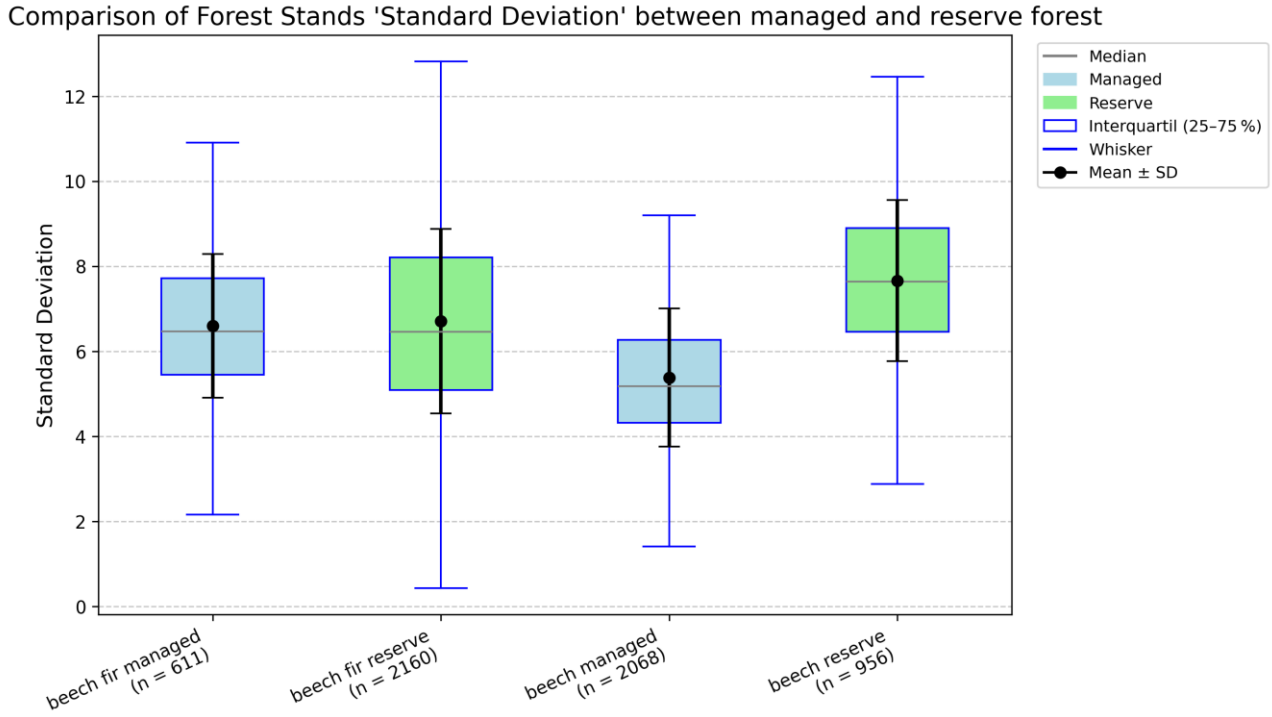


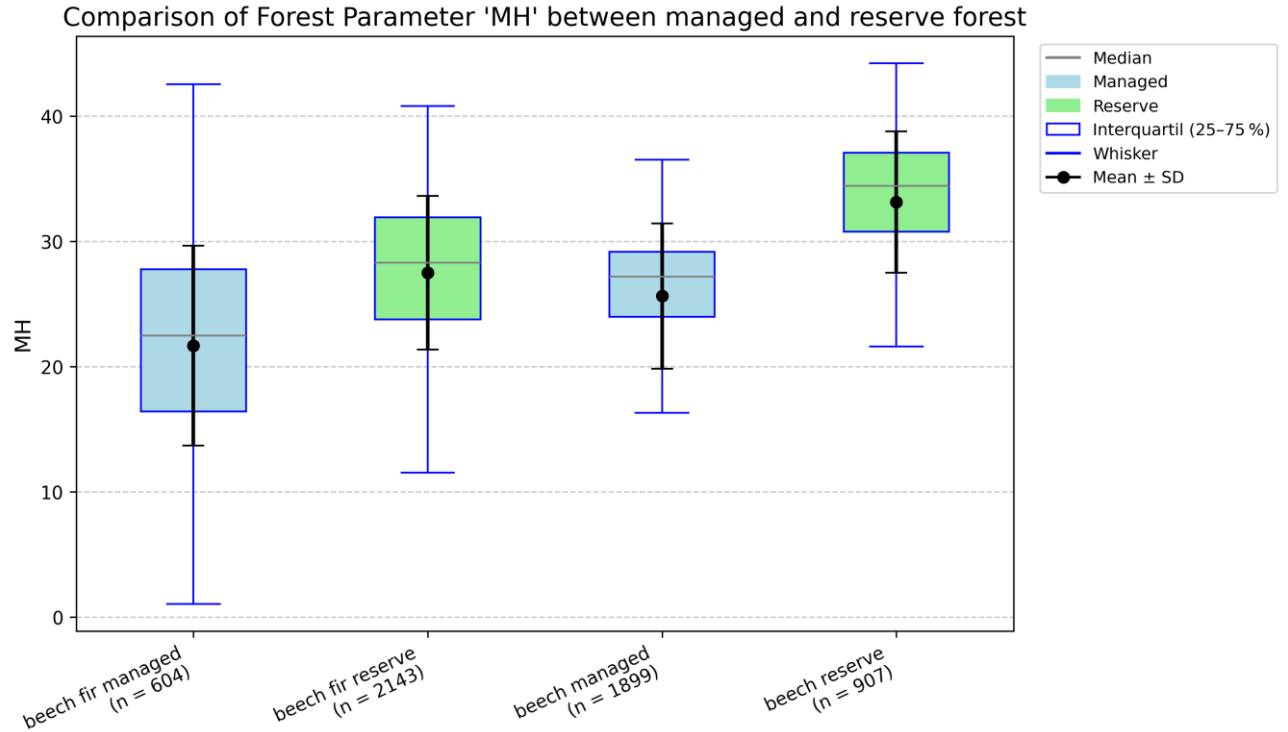

KOČEVJE
NOVO
MESTO


BREŽICE
2000
D96: 529.606,56 71.975,16 [m]

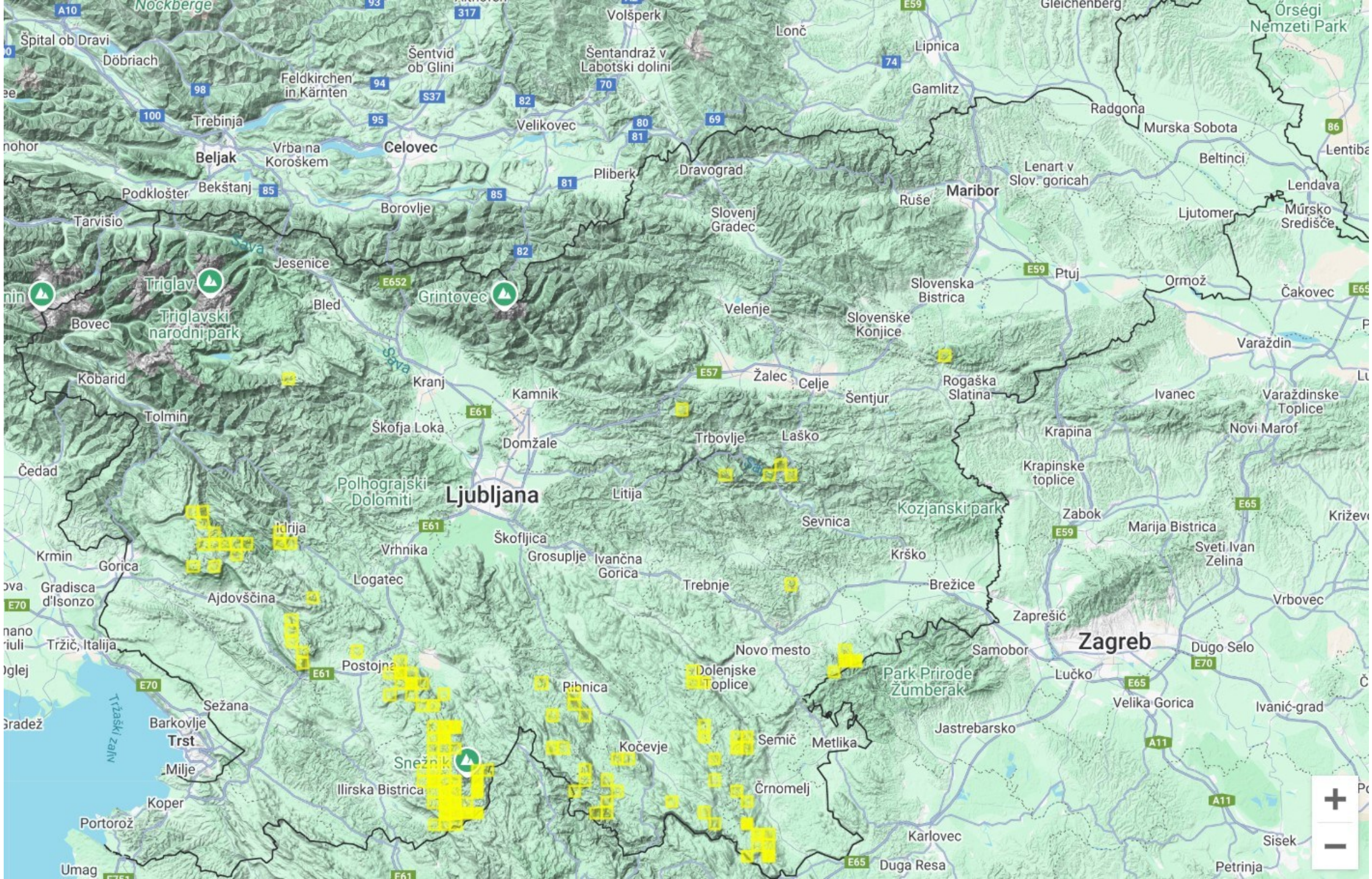


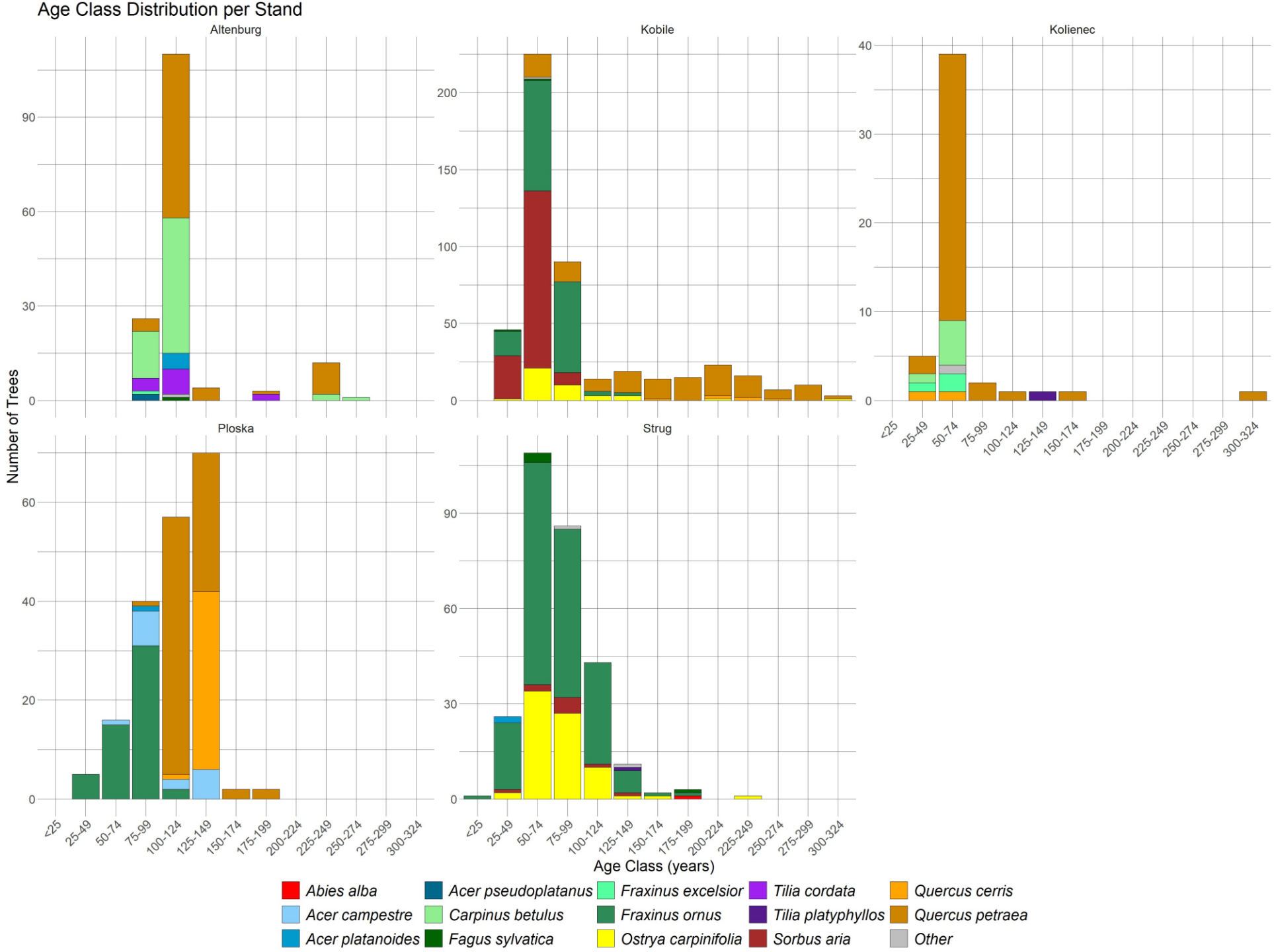

Kobile

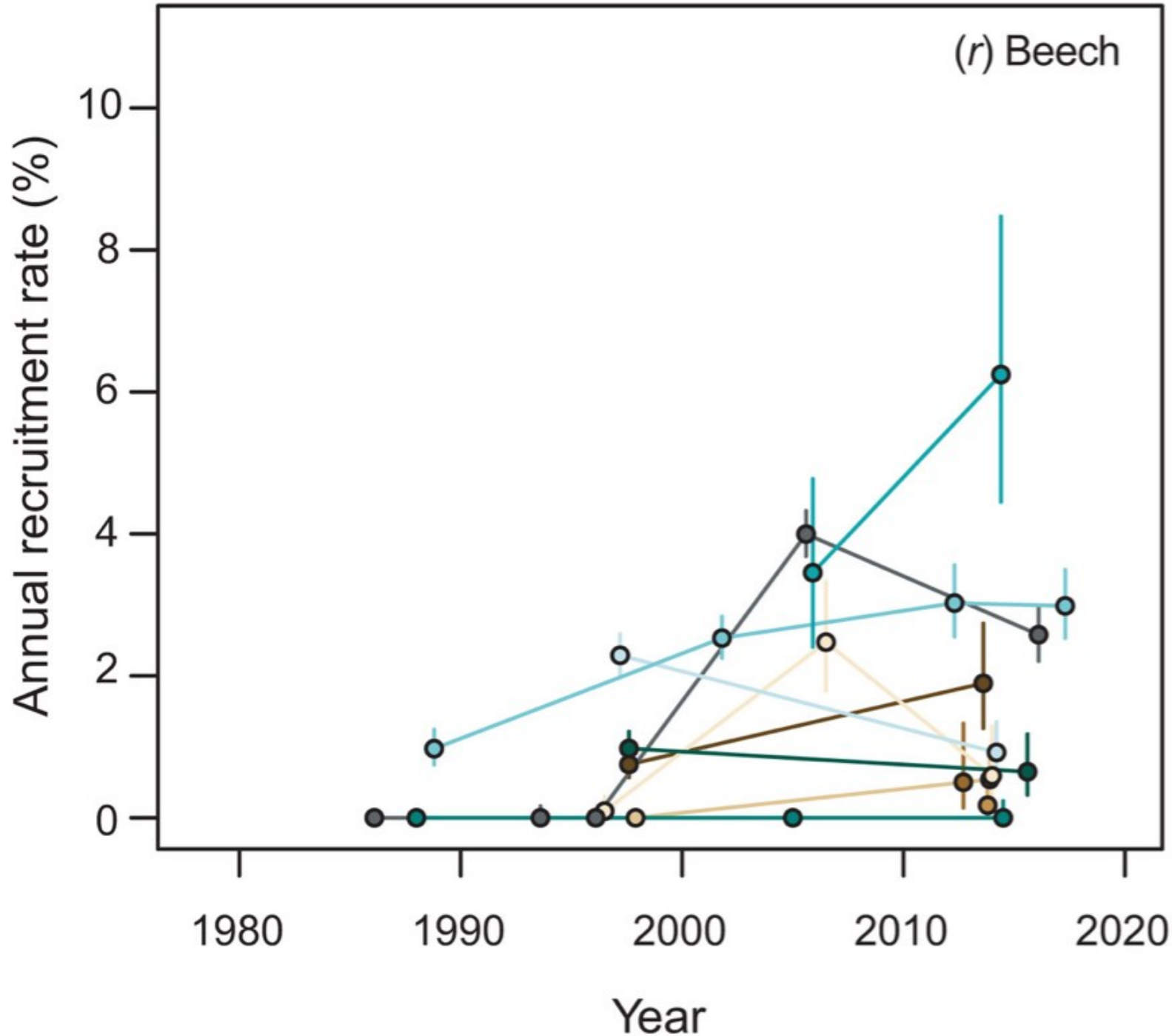


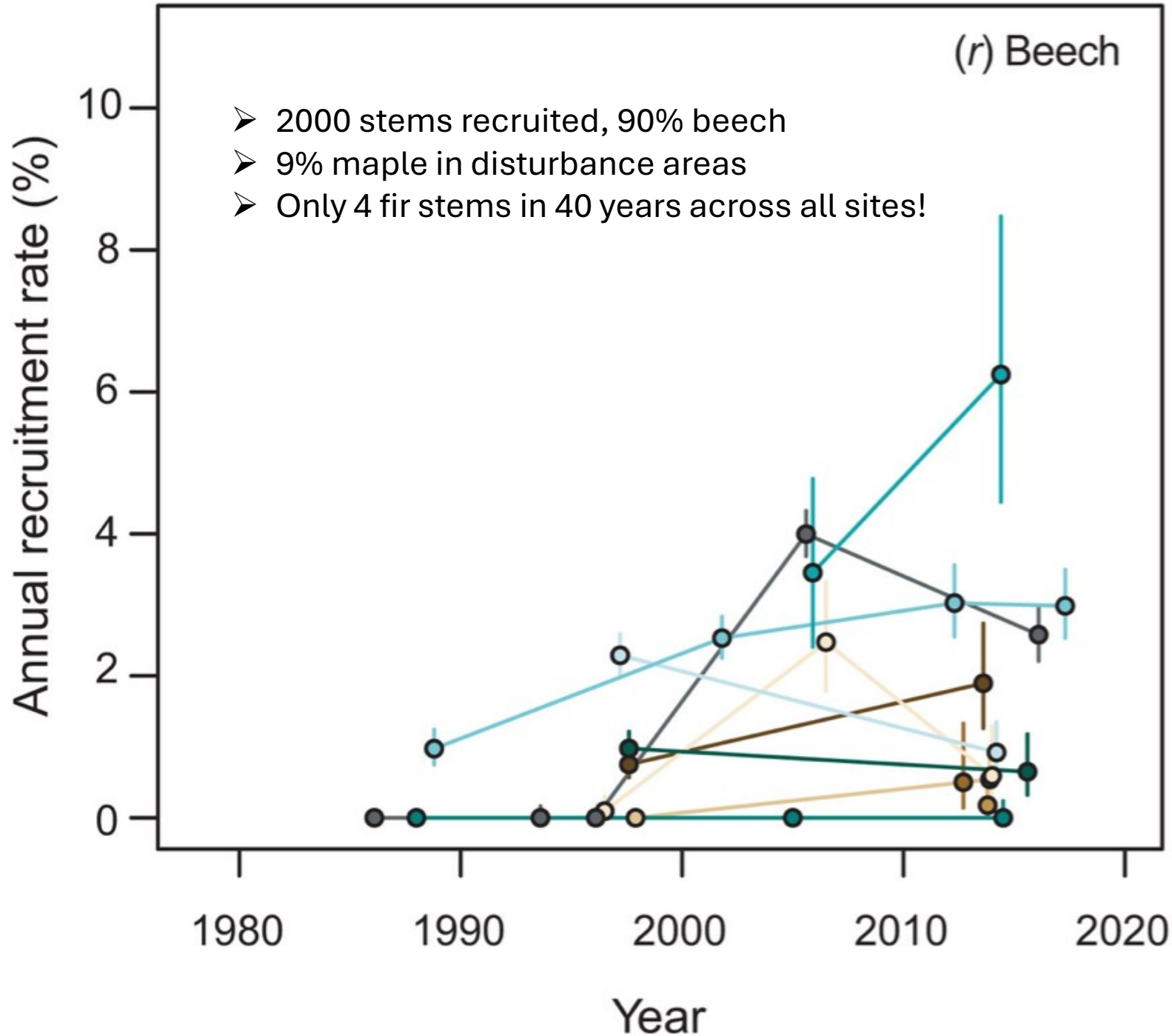




| Forest type | Percentage | Count | Gaps per ha | Mean size |
|---|---|---|---|---|
| Beech managed | 15.5% | 766 | 4.9 | 351.7 $m^2$ |
| Beech reserve | 7.6% | 589 | 10.2 | 76.4 $m^2$ |
| Beech fir managed | 37.3% | 175 | 5.02 | 778,1 $m^2$ |
| Beech fir reserve | 6.5% | 1078 | 7.7 | 85 $m^2$ |


Špital ob Dravi
Döbriach
Nockberge
Feldkirchen in Kärnten
Šentvid ob Glini
Volšperk
Šentandraž v Labotski dolini
Lonč
Lipnica
Gamlitz
Gleichenberg
Őrségi Nemzeti Park
Trebinja
Beljak
Vrba na Koroškem
Celovec
Velikovec
Radgona
Murska Sobota
Lenti
Podklošter
Bekštanj
Pliberk
Dravograd
Lenart v Slov. goricah
Beltinci
Lendava
Tarvisio
Borovlje
Slovenj Gradec
Ruše
Maribor
Ljutomer
Mürsko Središče
Jesenice
Triglav
Triglavski narodni park
Bovec
Bled
Grintovec
Ptuj
Ormož
Slovenska Bistrica
Čakovec
Velenje
Slovenske Konjice
Varaždin
Kobarid
Kranj
Kamnik
Žalec
Celje
Šentjur
Rogaška Slatina
Ivanec
Varaždinske Toplice
Tolmin
Škofja Loka
Domžale
Trbovlje
Laško
Krapina
Novi Marof
Čedad
Polhograjski Dolomiti
Ljubljana
Litija
Krapinske toplice
Kozjanski park
Zabok
Marija Bistrica
Križev
Idrija
Sevnica
Škofljica
Vrhnika
Grosuplje
Ivančna Gorica
Krško
Sveti Ivan Zelina
Krmin
Gorica
Logatec
Trebnje
Brežice
Gradisca d'Isonzo
Ajdovščina
Vrbovec
Zaprešić
Tržič, Italija
Novo mesto
Samobor
Zagreb
Dugo Selo
Postojna
Dolenjske Toplice
Park Prirode Žumberak
Lučko
Pivka
Sežana
Velika Gorica
Ivanić-grad
Barkovlje
Trst
Jastrebarsko
Kočevje
Semič
Metlika
Milje
Ilirska Bistrica
Črnomelj
Koper
Portorož
Karlovec
Sisek
Umag
Duga Resa
Petrinja


Age Class Distribution per Stand
Altenburg
Kobile
Kolienec
Ploska
Strug
Number of Trees
Age Class (years)
<25
25-49
50-74
75-99
100-124
125-149
150-174
175-199
200-224
225-249
250-274
275-299
300-324
Abies alba
Acer campestre
Acer platanoides
Acer pseudoplatanus
Carpinus betulus
Fagus sylvatica
Fraxinus excelsior
Fraxinus ornus
Ostrya carpinifolia
Tilia cordata
Tilia platyphyllos
Sorbus aria
Quercus cerris
Quercus petraea
Other


(r) Beech
Annual recruitment rate (%)
0
2
4
6
8
10
1980
1990
2000
2010
2020
Year




- 2000 stems recruited, 90% beech
- 9% maple in disturbance areas
- Only 4 fir stems in 40 years across all sites!

# Sasso Fratino, 2023

# Take home message

- Moderate severity, partial canopy disturbances are a key process in our temperate mountain forests
- Threats of increasing climate related tree mortality or disturbance in unmanaged forests are unfounded (at least for now)
- In fact, disturbance is desirable in forest reserves, but most reserves are too small to capture natural disturbance regimes and maintain disturbance dependent species.
- Currently, Europe probably does not protect enough unmanaged forests to maintain populations of more demanding old-growth species
- Increasing forest reserves has substantial co-benefit with long-term carbon storage
- Land sparing (Triad) may offer a viable solution to reconcile increasing demand for timber with conservation of native forest biodiversity
- Current progress in mapping and protecting high conservation value forests in Europe progressing too slowly
- Aside from climate change, deer browsing may be the most significant threat to our strict forest reserves!


59°
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FORESTE VETUSTE: STRUTTURA E BIODIVERSITÀ 2.0
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# THANK YOU!