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(Article begins on next page)

Title

Alternative stable states in mountain forest ecosystems: the case of European larch (*Larix decidua*) forests in the western Alps

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Abstract

European larch (*Larix decidua*) forests of the western Alps form extensive cultural landscapes whose resilience to global changes is currently unknown. Resilience describes the capacity of ecological systems to maintain a “stable state”, i.e. constant functions, processes, structure, and identity despite disturbances, environmental changes and internal fluctuations. Our aim is to explore the resilience of larch forests to changes in climate and land use in the western Italian Alps.

To do so, we assumed that mountain forests ecosystems can exist under alternative stable states. To describe quantitatively the larch forest state we used species tree basal area data obtained from field forest inventories in combination with topography, forest structure, land use, and climate information. To infer the resilience of larch forests relative to that of other forest states we applied three different probabilistic methods: frequency distributions, logistic regressions, and potential analyses.

We found patterns indicative of alternative stable states: bimodality in the frequency distribution of the percent of larch basal area, and the presence of an unstable state, i.e., transient mixed larch forests, in the potential analyses. We also found: (1) high frequency of pure larch forests at high elevation, (2) the probability of pure larch forests increased mostly with elevation, and (3) pure larch forests were a stable state in the upper montane and subalpine belts. Likewise, in the upper montane belt open canopy cover and high grazing pressure increased the frequency of larch forests.

Our study shows that the resilience of larch forests may increase with elevation, most likely due to the altitudinal effect on climate. Subalpine larch forests may be more resilient, and natural succession after land abandonment, e.g., towards *Pinus cembra* forests, seems slower than in montane larch forests. In contrast, in the upper montane belt only intense land use regimes characterized by open canopies and forest grazing may maintain larch forests. We conclude that similar approaches could be applied in other forest ecosystems to infer the relative resilience of tree species.

Keywords

Potential analysis; elevation; land use; natural succession; *Pinus cembra*; global change.

1. Introduction

Global change is affecting forest ecosystems worldwide. In mountains, land use changes are likely to have a greater impact than climate on forest structure and composition, and in turn, on the supply of ecosystem goods and services (Körner 2014). In the western Alps, European larch (*Larix decidua* Miller) forests are extensive cultural landscapes that provide diverse ecosystem services, such as timber production, landscape scenery, recreation, protection from hydrogeomorphic hazards, and biodiversity (Garbarino et al. 2011). In the last centuries, some land uses have strongly favored the dominance of larch over other tree species (Bourcet 1984). In particular, traditional silvopastoral activities such as timber harvesting, periodical pastoral fires, and heavy grazing have prevented natural succession and maintained landscapes dominated by larch (Holtmeier 1995; Schulze et al. 2007) by creating suitable conditions for its natural regeneration, i.e., open canopies and mineral soil exposure (larch is a light-demanding, pioneer species that regenerates on bare soil) (Holtmeier 1995; Schulze et al. 2007). However, a strong reduction in population density and grazing pressure occurred in the 20th century, and nowadays forest grazing is not anymore the most important service of these forests (Garbarino et al. 2011). In the same period, pastoral fires have been banned and fire suppression policies have markedly reduced fire occurrence. In the absence of such historical land uses, other species such as *Picea abies*, *Abies alba* and *Pinus cembra* dominate the current natural regeneration (Motta and Dotta 1995), and the resilience of larch forests has been questioned (Bonnassieux 2001).

Resilience can be defined as the capacity of a system to absorb disturbances, environmental changes, and fluctuations in its internal components, and still retain the same state, i.e. function, processes, structure and identity (Holling 1973; Walker et al. 2004; Mumby et al 2014). Shifts from one state of the system to another can result from diverse causes: exogenous disturbances, gradual changes in environmental conditions, endogenous processes, or any combination of the three (Scheffer and Carpenter 2003; Staal et al. 2015). Indeed, resilience can be used to measure the probability that a system remains stable given a particular change (Holling 1973; Peterson 2002; Beisner 2012; Mumby et al. 2014).

Systems can also exist in multiple, or “alternative”, stable states under the same set of environmental conditions (Beisner et al. 2003; Schröder et al. 2005; Petraitis 2013; Kéfi et al. 2016), for example in stochastic environments with strong disturbances. Theoretically, such systems are more often found close to attractors (stable states) than around repellors (unstable states) (Scheffer et al. 2015). This has important practical implications for the quantitative analysis of resilience. First, frequency distributions of the state variable can be used to approximate the shapes of basins of attraction that compose the “stability landscape” (Scheffer et al. 2012a, 2015). Second, the probability of finding a given state is indicative of its resilience, because states with bigger basins of attraction have higher chances to persist despite disturbances (Hirota et al. 2011; Scheffer et al. 2012b, 2015). Third, it is possible to reconstruct stability landscapes (i.e., representations of the basins of attraction) using potential analysis based on temporal and spatial datasets (Livina et al. 2010; Hirota et al. 2011; Scheffer et al. 2012b, 2015). These probabilistic methods infer relative resilience, i.e., the resilience of one state is relative to that of other states (Scheffer et al. 2015).

Our aim is to explore the resilience of European larch forests to changes in climate and land use in the western Italian Alps. To do this, we considered larch forests as an alternative stable state of mountain forest ecosystems along an elevation gradient, and used larch basal-area dominance as the state variable. We applied frequency distributions, logistic regressions, and potential analyses to tree data obtained from field forest inventories in combination with topography, forest structure, land use, and climate information. We suggest that similar approaches can be applied in other forest ecosystems.

2. Materials and methods

2.1. State variable and drivers

To calculate the state variable of larch forests we used data from 7305 plots of the forest inventories of Aosta Valley and Piedmont regions in northwestern Italy (Figure 1). The forest inventories were conducted between 1993 and 2003 using similar survey protocols. Species was identified and the diameter at breast height (dbh) was measured from all the living trees with dbh > 7.5 cm inside circular plots with a variable radius between 8-15 m depending on tree density.

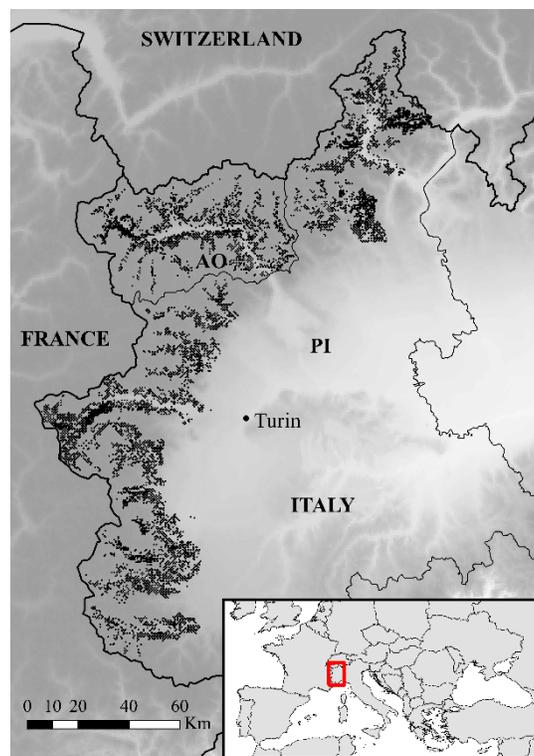


Figure 1. Distribution of 7305 forest inventory plots (black dots) in the regions of Piedmont (PI) and Aosta Valley (AO) in Italy.

We chose the percent of larch basal area in the plot as state variable. Indeed, basal area is an integrative descriptor of forest structure in larch forests (Garbarino et al. 2009). We considered 13 potential drivers of larch resilience (Table 1). These variables are proxies of the factors that influence the distribution of European larch forests, i.e., topography, forest structure, land use, and climate (Caccianiga et al. 2008; Garbarino et al. 2009, 2011, 2013). We did not want to

inflate the state variable with zero values by extending the study area where European larch is absent. Thereby, we did not include plots from forest districts in Piedmont where the cover of larch forests was < 5% of the total forest area.

Table 1. State variable and potential drivers of European larch resilience.

Variable	Unit	Description	Source
State:			
Larix	%	Proportion of <i>Larix decidua</i> in the total basal area of the plot	Calculated from RFI
Topography:			
Elevation	m	Meters above sea level	RFI
Slope	°	Steepness of terrain	RFI
Aspect	Factor	North, East, South, West	RFI
Forest structure:			
Canopy cover	%	Proportion of forest floor covered by tree crowns	RFI
Basal area	m ² /ha	Land occupied by the cross-section of tree stems at 1.3 m	RFI
Land use:			
Pasture	Factor	Domestic animals, wild ungulates, no signs	RFI
Grazing	%	Proportion of area covered by only herbaceous and shrub vegetation within a 200-m-radius area from the plot center	CORINE land cover
Climate:			
Annual precipitation	mm	Annual precipitation	Global Climate Data
Mean annual temperature	°C	Mean annual temperature	Global Climate Data
Mean temperature July	°C	Mean temperature in July	Global Climate Data
Mean temperature January	°C	Mean temperature in January	Global Climate Data
Gams index	°	Annual precipitation/Elevation	Calculated from GCD
Icc		Temp July – Temp January + (Elevation*0.6/100)	Calculated from GCD

Icc: Compensated Continentality Index; RFIs: Regional Forest Inventories; CORINE land cover: European land use classes map in 1990; Global Climate Data (GCD): set of climate grids with a spatial resolution of 1 Km² for the period 1950-2000 (Hijmans et al. 2005).

2.2. Methods of analysis

We carried out three kinds of analyses to explore the resilience of larch forests: (1) frequency distributions to detect changes in the modality of the state variable, (2) logistic regressions to estimate probabilities of finding pure larch forests, and (3) potential analyses to detect stable and unstable states, and provide a qualitative estimation of the resilience of larch forests. We

performed all the analyses within the R statistical framework (R Core Team 2014), except in the case of potential analyses where we also used MATLAB R2014b. The datasets and R scripts are available in Appendix B.

2.3. Frequency distributions

We first divided the dataset into four elevation belts: > 1900 m (subalpine), 1400-1900 m (upper montane), 900-1400 m (lower montane), and < 900 m (lowland). We additionally divided each driver into four levels to see how relative frequency distributions of the state variable varied along elevation and those four levels of each driver.

2.4. Logistic regressions

First, we explored collinearity between drivers with Pearson's r correlation coefficients and boxplots. We excluded variables from further analyses when $r > 0.6$. Beforehand, we divided the plots into two classes to create the response variable for the logistic regressions. We grouped together plots where the percent of larch basal area was > 75%, which represented pure larch forest stands (value = 1; in the rest of the plots value = 0). We ran a logistic regression with six drivers and checked for quadratic terms and interactions among drivers (Hosmer and Lemeshow 2000). We assessed the goodness-of-fit of the model with the Nagelkerke R^2 and the area under the curve (AUC), and the relative importance of the drivers with hierarchical partitioning. Finally, we ran logistic regressions with different thresholds for the definition of pure larch, i.e., from 55% to 95% larch basal area, to assess how such thresholds affected statistical significance and relative importance of the drivers.

2.5. Potential analyses

Potential analysis is a method developed to detect the number of states in non-linear dynamical systems affected by stochastic processes (Livina et al. 2010). The potential function, derived from a probability density function, only requires data on the state variable and one driver (or time). Potential values, obtained from the potential function, are equivalent to the height of the stability landscape, and thus it is possible to compute stability landscapes along the gradient of the driver, obtaining a potential landscape (Hirota et al. 2011; Scheffer et al. 2012b). Local minima and maxima in the potential landscape correspond to attractors (stable states) and repellers (unstable states) respectively. Potential landscapes are useful to know the number of states in a system, detect alternative stable states, and estimate resilience qualitatively. We used the function *movpotential_ews* from the package *earlywarnings* in R to build potential landscapes (Dakos et al. 2012). We followed Hirota et al. (2011) and Scheffer et al. (2012b) to detect local minima and maxima by using the same code in MATLAB and a threshold value = 0.002.

We first computed a potential landscape using all the forest inventory plots and elevation as the main driver. We wanted to know how other drivers influenced the potential landscape. Therefore, we divided the dataset into four levels for each driver, in the same way we did with frequency distributions. We then computed potential landscapes (always using elevation as driver) from

these partial datasets, for example from plots where canopy cover > 80%, or from plots where grazing < 25%.

Forests of *Pinus cembra* are potentially a later seral stage in the succession of subalpine larch forests (Ozenda 1985). We performed a potential analysis with data coming only from the forest district of Varaita Valley (Figure A1), where is located the largest forest of *Pinus cembra* in the western Italian Alps. Finally, we divided the dataset into two climate sectors (Camerano et al. 2007, 2008) (Figure A1), endalpic (more continental) and mesalpic (more oceanic), and computed a potential landscape for each sector.

3. Results

3.1. Frequency distributions

The relative frequency distribution of the state variable was bimodal with two peaks around 0 and 100%, and low frequencies in the rest of the range (Figure A2). Both peaks represented two different states: a state with no larch, and a pure larch state. The frequency distribution of the state variable varied strongly with elevation (Figure 2): at low elevation (lowland and lower montane) the non-larch state was the most frequent, and on the contrary, at high elevation (subalpine) the pure larch state dominated (unimodal distribution). In the upper montane belt (1400-1900 m) the distribution of larch basal area was bimodal (Figure 2). Larch dominated more where the presence of domestic animals was confirmed and where canopy cover was low (Figure 3). These patterns were weaker in the lower montane and subalpine belts, but clearer in the upper montane elevation range (Figure 3).

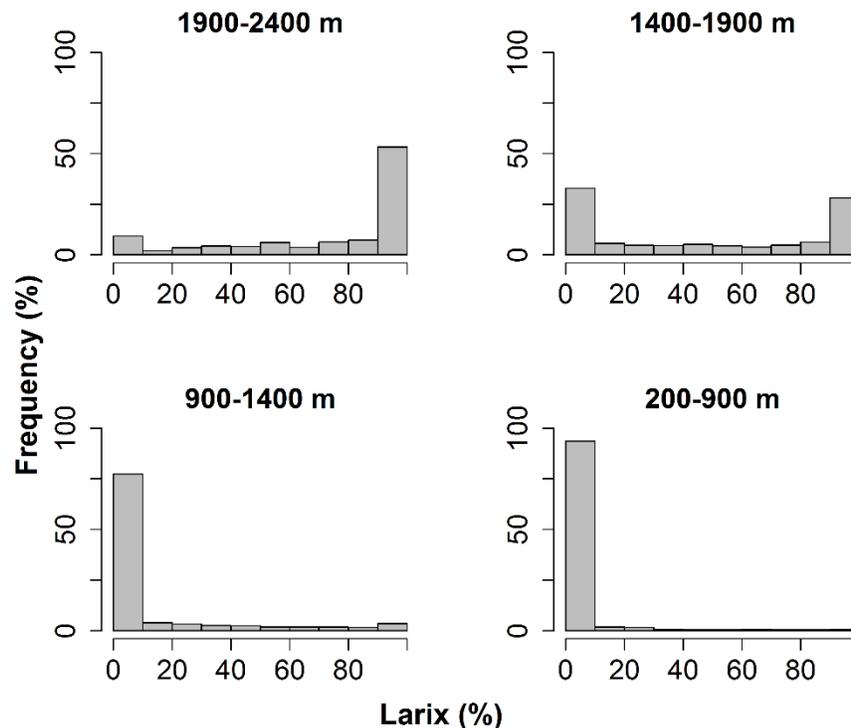


Figure 2. Relative frequency distributions of the state variable in different elevation belts: subalpine (1900-2400 m), upper montane (1400-1900 m), lower montane (900-1400 m) and lowland (200-900 m).

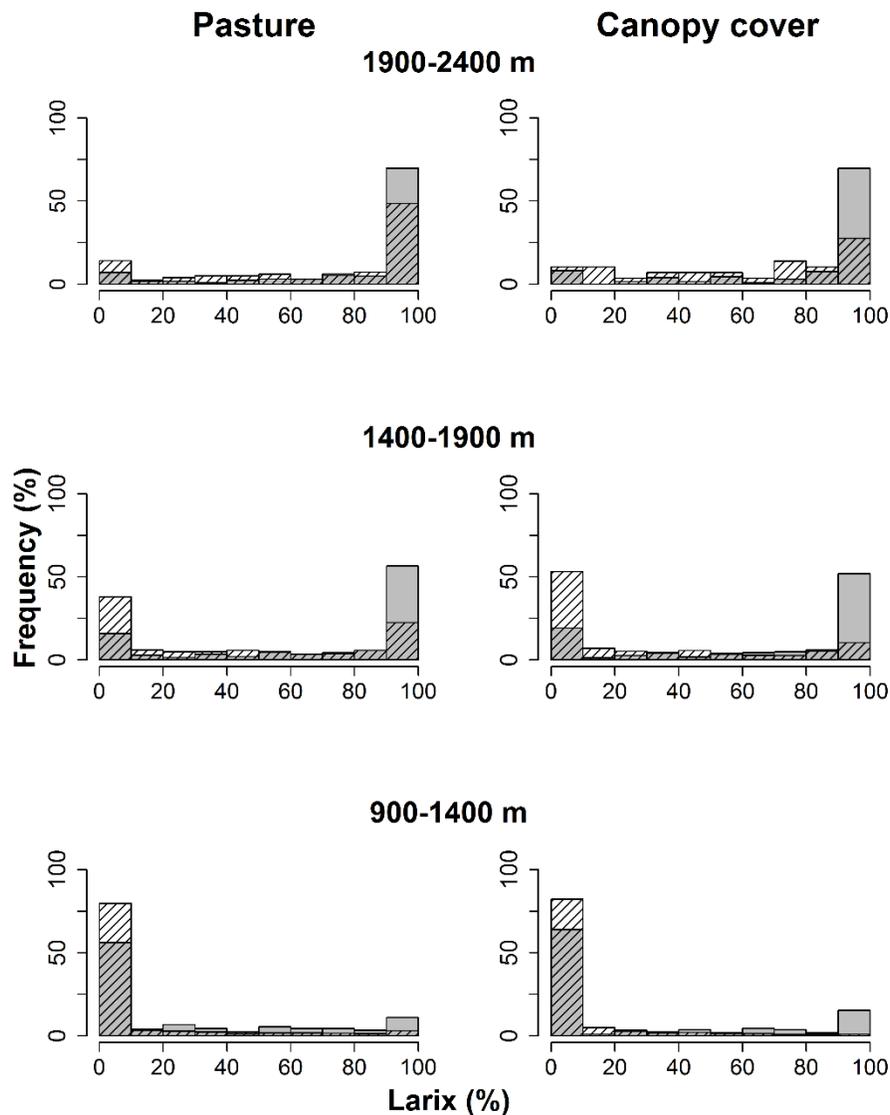


Figure 3. Relative frequency distributions of the state variable in different elevation belts and levels of two drivers: pasture and canopy cover. Grey bars represent presence of domestic animal signs (left) and 20-40% canopy cover (right), while dashed bars represent absence of animal signs (left) and 80-100% canopy cover (right).

3.2. Logistic regressions

There was a strong correlation between elevation and all the climate variables (Table A1), and so we did not include climate variables in the logistic regressions. We selected elevation instead of any climate variable because we can know elevation accurately at small scale, while climate variables are generated through interpolation of data from weather stations at higher spatial scale. We also dropped pasture due to collinearity with elevation, canopy cover, and grazing.

The probability of finding pure larch forest stands increased with elevation, grazing pressure and in north slopes, while decreased with canopy cover and in south slopes (Table 2). Slope and basal area were not significant predictors (Table 2). Goodness-of-fit of the model: Nagelkerke $R^2 = 0.467$ and AUC = 0.890. Elevation was the most important variable explaining the presence of pure larch forests, followed by canopy cover and grazing pressure (Table 2). The threshold value used to define pure larch stands did not affect either statistical significance or relative importance of the drivers in the logistic regressions.

Table 2. Summary of the logistic regression model.

Variable	Coefficient	Std. error	z value	p value	rel. imp. (%)
Elevation	0.003	0.000	28.701	< 0.001	66.2
Slope	-0.009	0.004	-2.366	0.018	0.2
Aspect North	0.399	0.105	3.814	< 0.001	3.6
Aspect West	0.079	0.113	0.702	0.483	
Aspect South	-0.647	0.126	-5.149	< 0.001	
Canopy cover	-0.023	0.002	-11.445	< 0.001	18.1
Basal area	-0.002	0.003	-0.551	0.582	1.4
Grazing	0.010	0.001	8.493	< 0.001	10.5

Significant results in bold (alpha = 0.01); rel. imp. (relative importance): proportion of the total explained variance.

3.3. Potential analyses

In the potential landscape computed from the whole dataset with elevation as driver (Figure 4), we detected two states, which are represented by two main series of local minima (i.e., attractors). One corresponded to pure larch forests (red dots at the top of Figure 4), and the second state corresponded to other forests in the study area, e.g., *Pinus sylvestris*, *Picea abies* or *Fagus sylvatica* (red dots at the bottom of Figure 4). We also detected an unstable state, which is represented by local maxima (i.e., repellers; blue diamonds in the center of Figure 4), and corresponded to mixed larch forests. The overlap of both stable states (pure larch and non-larch) generated a bistability range in the upper montane belt (approximately 1400-1900 m). On the other hand, in the subalpine belt (> 1900 m) only pure larch appeared as attractor, whereas in the lower montane and lowland belts (< 1400 m) only non-larch attractors were present.

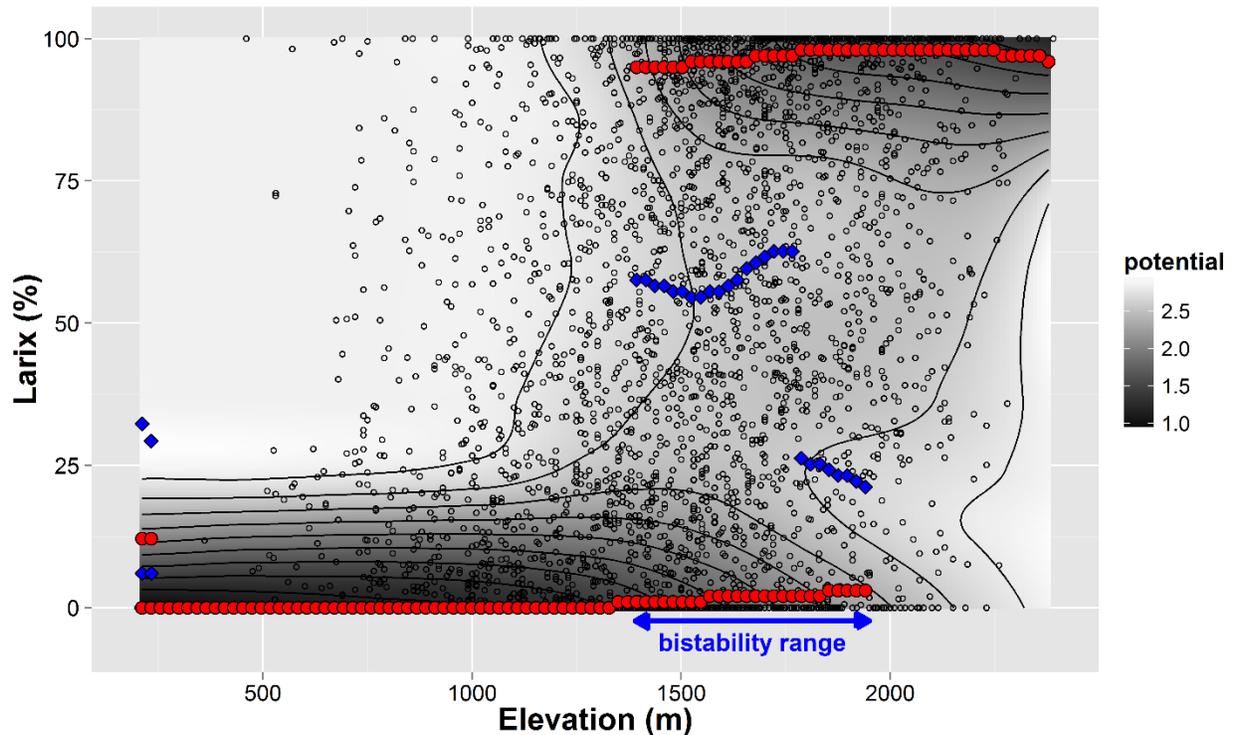


Figure 4. Potential landscape and local minima (red dots) and maxima (blue diamonds) computed using the state variable (i.e., the percent of larch basal area), and elevation as driver. Empty dots represent 7305 forest inventory plots. Lines represent isocurves of potential. Both stable states correspond to two groups of local minima: at the top the pure larch state, and at the bottom the non-larch state. The group of local maxima in the center symbolizes an unstable stable (i.e., mixed larch forests). The blue arrow indicates the overlap of both stable states in the upper montane belt (bistability range).

We observed two types of changes in potential landscapes computed from partial datasets (Figure 5): (1) the degree of overlap between stable states, and (2) its position along the elevation gradient. For instance, when canopy cover > 80% (Figure 5D), the bistability range decreased and moved towards higher elevation. On the other hand, when grazing > 75% (Figure 5E), the bistability range shifted towards lower elevation.

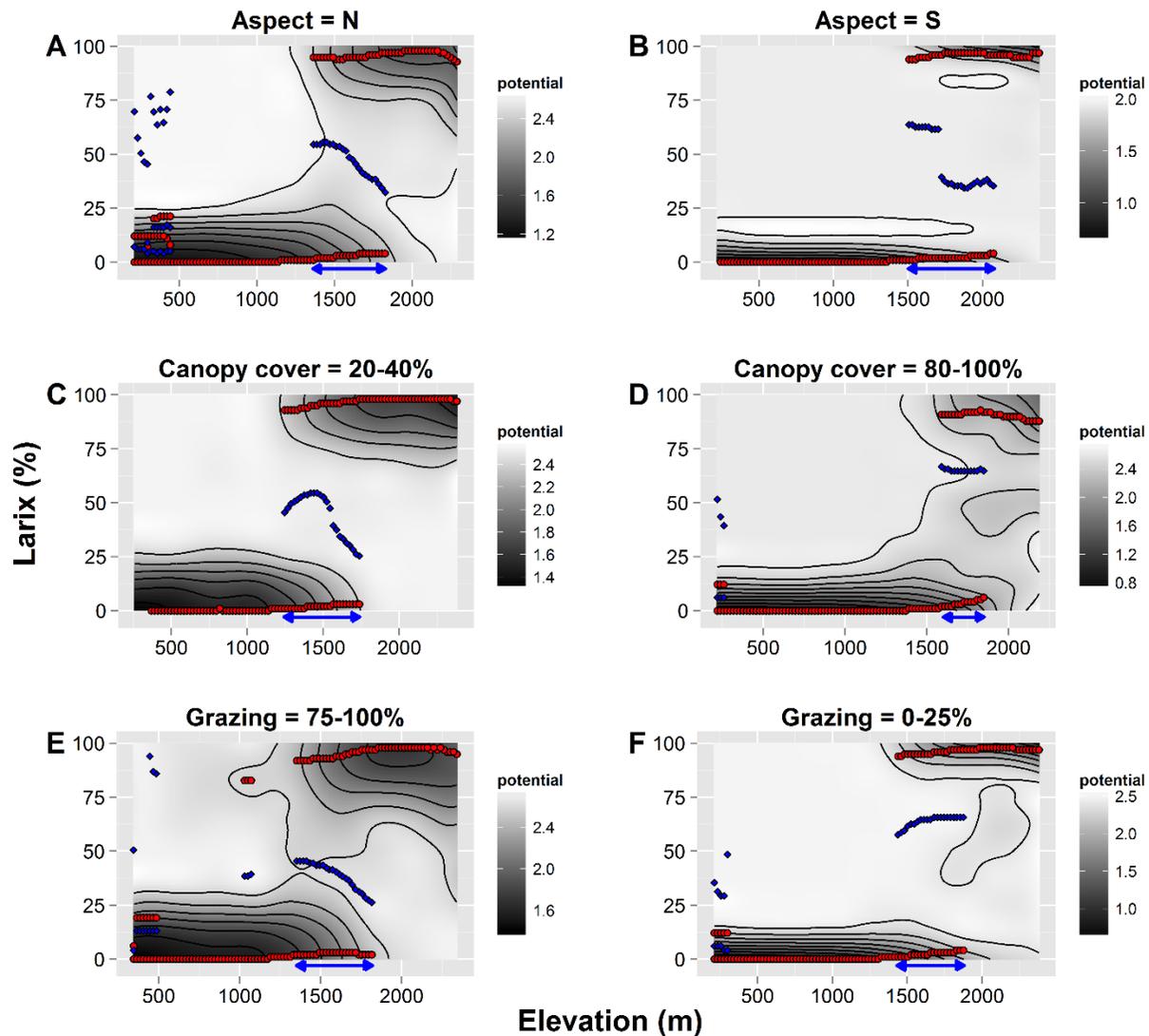


Figure 5. Potential landscapes and local minima (red dots) and maxima (blue diamonds) computed from partial datasets using the state variable (i.e., the percent of larch basal area), and elevation as driver. The blue arrow indicates the bistability range.

The potential landscape of Varaita Valley showed a third stable state, i.e., cembran pine forest (Figure 6). In fact, at high elevation cembran pine was the only stable state and we did not detect the pure larch state in the subalpine range. We suspect that this may be due to the small dataset used in the analysis (only 313 plots), and an overlap between larch and cembran pine could be detected in if more plots were available. On the other side, bistability took place at lower elevation in the endalpic potential landscape (Figure 7 right) than in the mesalpic potential landscape (Figure 7 left).

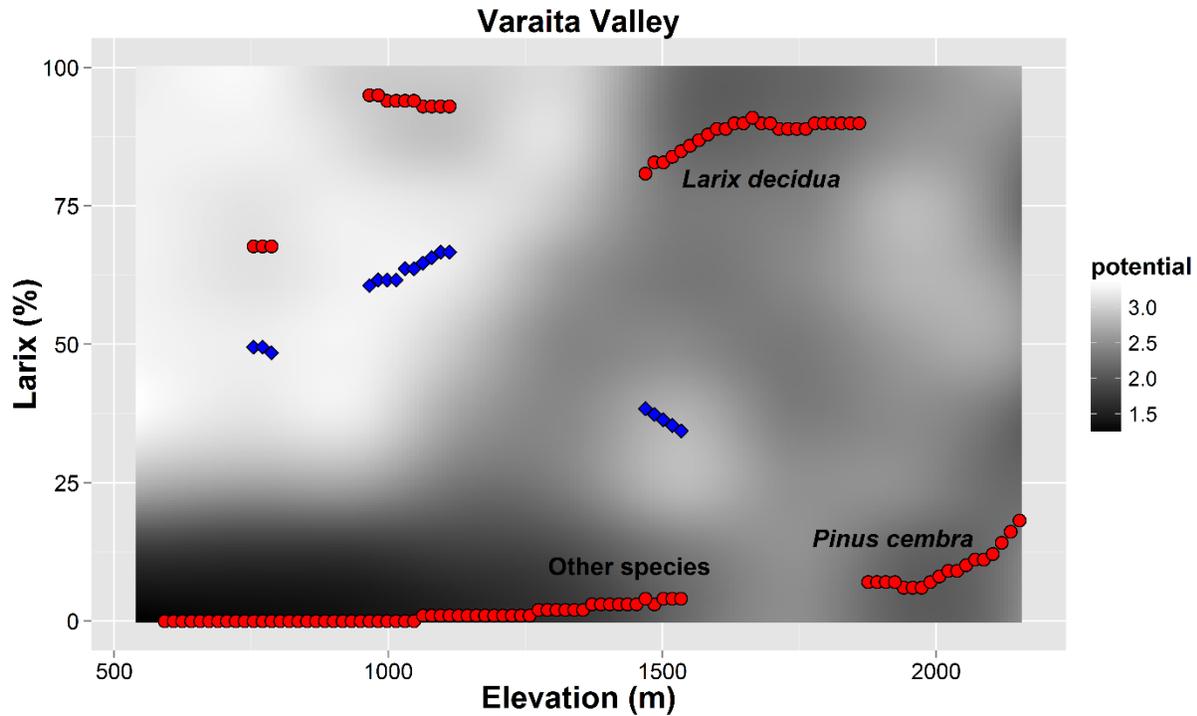


Figure 6. Potential landscape and local minima (red dots) and maxima (blue diamonds) of Varaita Valley.

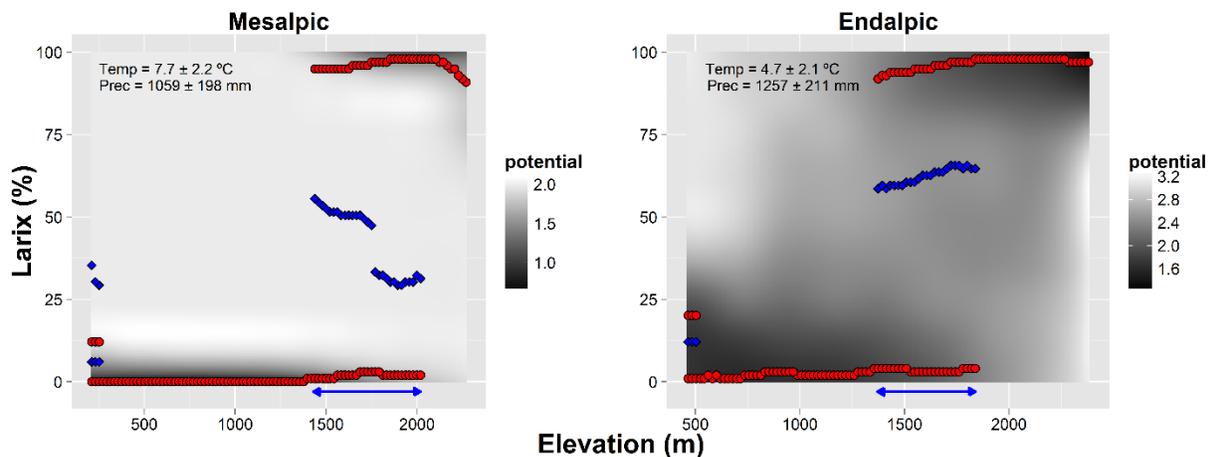


Figure 7. Potential landscapes and local minima (red dots) and maxima (blue diamonds) of the mesalpic (left) and endalpic (right) climate sectors. Blue arrow: bistability range. Temp: mean annual temperature (mean \pm sd); Prec: annual precipitation (mean \pm sd).

4. Discussion

4.1. Alternative stable states and relative resilience

Our results suggest that ecosystems of the western Italian Alps display alternative stable states in relation to larch dominance. We found two patterns indicative of the existence of alternative stable states (Petraitis 2013): (1) bimodality in the frequency distribution of the state variable,

i.e., larch dominance (Figure A2), and (2) the presence of an unstable state (mixed larch forests) in the potential landscape, which implies the presence of two alternative stable states (pure larch, or absence of larch) under similar environmental conditions (Figure 4). In the lower montane belt, pure larch forests were infrequent at any level of either grazing pressure or canopy cover (Figure 3). In contrast, in the upper montane belt, open canopy cover and high grazing pressure increased notably the frequency of pure larch forests, whereas in closed forests and under low grazing pressure the frequency of pure larch forest decreased (Figure 3). At subalpine elevations larch dominated ubiquitously (Figure 3), which suggests that high elevation climate reduces considerably the probability of shifts from larch forests to other forest composition, despite changes in the land use regime. In summary, larch forests occur along a wide elevation range, but only in the upper montane and subalpine belts they represent a stable state. In the upper montane belt, it seems that land use is an important factor driving the occurrence of either of the two alternative stable states (Staver et al. 2011; Dantas et al. 2015). Therefore, the persistence of larch forests most likely depends on the interplay between climatic conditions and land use regime.

To interpret resilience from the results, we made some assumptions based on generic properties of ecological systems with alternative stable states (Scheffer and Carpenter 2003; Hirota et al. 2011; Scheffer et al. 2012b, 2015; Dakos et al. 2015). First, systems tend to occur more frequently in states that are more resilient. Consequently, the high frequency of pure larch forests at high elevation may reflect its high relative resilience in the subalpine belt (Figure 2). Second, probabilities from logistic regression can be interpreted as likelihoods of persisting in a given state, i.e., as numerical indicators of relative resilience. Our logistic model suggests that mostly elevation, but also grazing pressure and canopy openness may increase larch resilience (Table 2). Third, relative resilience declines towards bifurcation points, i.e., the extreme attractor points in the bistability range of the potential landscape. In our dataset, pure larch forests became more likely with increasing elevation (Figure 4), and the inferred bistability range was displaced, enlarged, or shortened by several drivers (Figure 5) (van Nes et al. 2014). Therefore, relative resilience of larch forests increased with elevation and may be higher on north slopes, at low canopy cover, and high grazing pressure.

Resilience may be easy to understand but difficult to evaluate, especially in slow-responding systems like forests (Reyer et al. 2015). We applied a combination of different probabilistic methods searching for multiple evidences that converged on the same kind of conclusion (Scheffer and Carpenter 2003). The probabilistic resilience that we inferred in this study must be interpreted as a generic resilience of larch forests to state shifts, either slow such as forest succession, or sudden such as natural disturbances. However, we need further research on the impact of specific disturbances on larch forests to confirm that the studied drivers affect larch resilience to different disturbance agents (e.g., forest fires or snow avalanches) in the same way we presented here.

4.2. Driving factors of European larch forests

Elevation was a key variable to explain the distribution of European larch forests. In the Alps, air temperature decreases linearly with elevation, while the positive relationship between elevation and precipitation can vary regionally in different ways (Ozenda 1985; Sevruk 1997; Körner

2007). Continental conditions are suitable for larch, and European larch forests find these conditions in the subalpine belt (Ozenda 1985). Potential analyses of endalpic and mesalpic climatic sectors (Figure 7) pointed in the same direction: resilience of European larch forests increases with continentality. Furthermore, potential landscapes with Gams index and Icc (i.e., hygric and thermal bioclimatic indices of continentality respectively) as drivers (Figure A3) showed similar patterns to the ones obtained with elevation (Figure 4). Therefore, the fact that elevation may be the main driver of larch forests resilience most likely comes from the elevation effect on climate, especially regarding temperature. In the Alps, temperatures are projected to increase during the 21st century (Zimmermann et al. 2013; Gobiet et al. 2014), and climate change is expected to reduce the area with suitable climatic conditions for European larch (Casalegno et al. 2010; <http://forest.jrc.ec.europa.eu/activities/climate-change/species-suitability/>). Consequently, under global warming, we expect that the resilience of European larch forests will decline.

Decreasing grazing is the main driver of the current dynamics of larch forests in the western Alps (Motta and Nola 2001; Motta and Edouard 2005; Motta and Lingua 2005; Motta et al. 2006). Nowadays, montane and low elevation larch forests are being replaced by other tree species (Motta and Dotta 1995), whereas larch colonizes abandoned subalpine pastures and the treeline (Didier 2001). However, this upward displacement seems to be caused mainly by land abandonment, that exceeds the effects of climate warming by allowing forest maturation and succession (Bodin et al. 2013) and an upward shift of the treeline (Gehrig-Fasel et al. 2007). In European larch forests, low basal area and canopy cover are indicators of strong human influence (Garbarino et al. 2011), and could be utilized as proxies of land use. Our results indicate that human activities, such as forest grazing, seem to be important to maintain larch forests, especially in the upper montane belt (Figure 3). Nevertheless, it is likely that our results underestimate the effects of land use because: (1) the proxies are not able to fully capture the historical intensity of grazing, and (2) high levels of grazing pressure are underrepresented in the dataset due to the current abandonment of alpine farming.

In the western Alps, larch has a pioneer role in the forest succession, and is considered a temporary seral stage in the succession towards other forest types (Motta and Dotta 1995; Bonnasiuex 2001). Our results show that mixed-larch forests are unstable states (Figure 4), and probably most of them are in transition from pure larch stands to other forest types. Pure larch forests were the only stable state detected in the subalpine belt (Figure 4); however, the slow rate of species change in subalpine areas forests may make larch forests appear more resilient than they actually are (Ratajczak and Nippert 2012). On the other side, traditional silvopastoral activities have been crucial to slow down and interrupt natural succession (Holtmeier 1995; Schulze et al. 2007) by (1) maintaining open structures that favored the regeneration of larch, (2) promoting larch establishment on bare soil, or (3) removing all regeneration in larch stands. Therefore, when traditional silvopastoral management is abandoned, natural regeneration from other tree species invades larch stands, at faster rates in montane larch forests (Motta and Dotta 1995).

Silvopastoral activities eliminated *Pinus cembra* during centuries, to the point that it was almost removed from the alpine forest landscape (Holtmeier 1990, 1994; Boden et al. 2010). However,

due to land abandonment, cembran pine is gradually replacing larch at high elevation, although the succession is slow and mixed larch-cembran pine stands can persist for centuries (Motta and Nola 2001; Motta and Lingua 2005; Motta et al. 2006). Cembran pine is considered a typical species of advance successional stages in subalpine forests (Bonnasieux 2011), but is also able to colonize abandoned subalpine pastures and the treeline because (Holtmeier 1990): (1) a dense cover of grasses and dwarf shrubs does not prevent its regeneration, and (2) its seeds are mainly dispersed by a bird, the European nutcracker (*Nucifraga caryocatactes*). We could not detect any state that represented cembran pine forests because its presence in the dataset was very rare with the exception of Varaita Valley (Figure 6). Nonetheless, cembran pine forests may be an alternative stable state in the subalpine belt, and may finally dominate where larch forests undergo land abandonment for long periods (Figure A4).

5. Conclusions

Elevation is probably the main driver of larch forests resilience to land use and climate changes in the Western European Alps. Resilience may increase with elevation because climate becomes more continental at high altitudes. However, larch resilience may be contingent upon diverse drivers. For instance, resilience could be higher in north slopes and open larch forests. European larch forests (Figure A5) are possibly alternative stable states in the western Alps. In the subalpine belt, larch forests may be more resilient, and thus natural succession after land abandonment is slower than in lower elevation ranges. Conversely, in the upper montane belt, only intense land use regimes seem to maintain larch forests. We expect climate change to decrease larch forests resilience, while land use changes will most likely reduce the extension of montane larch forests. At the same time, global warming and land abandonment are expected to govern the colonization of subalpine pastures and the tree line by mainly larch and cembran pine.

In this study, we provide an example of how to infer a generic relative resilience of a single tree species without information on forest disturbances. We used data from field forest inventories and combined three different methods, i.e., frequency distributions, logistic regressions, and potential analyses. Similar approaches can be applied from regional to national and continental scales. If data about the state variable (e.g., a tree species or a forest type) and drivers are not available from traditional forest inventories, perhaps such data can be obtained by other means, e.g., remote sensing. This approach could help to prepare forest resilience maps, showing where changes in forest species are more likely under diverse scenarios.

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Appendix A. Supplementary material

Table A1. Pearson's r correlation coefficients between continuous variables.

	Elevation	Slope	Cover	BA	Grazing	Prec	Temp	T Jul	T Jan	Gams	Icc
Larix	0.62	-0.02	-0.40	-0.05	0.28	0.41	-0.55	-0.56	-0.55	0.46	0.62
Elevation		0.07	-0.37	0.04	0.30	0.69	-0.89	-0.90	-0.85	0.81	0.96
Slope			0.06	-0.03	-0.01	0.12	-0.10	-0.10	-0.09	0.06	0.05
Cover				0.35	-0.27	-0.23	0.33	0.33	0.32	-0.29	-0.37
BA					-0.15	0.03	-0.03	-0.03	-0.04	0.06	0.05
Grazing						0.24	-0.32	-0.32	-0.30	0.20	0.27
Prec							-0.90	-0.88	-0.90	0.18	0.62
Temp								1.00	0.98	-0.53	-0.82
T Jul									0.97	-0.56	-0.82
T Jan										-0.47	-0.82
Gams											0.79

r > 0.6 in bold.

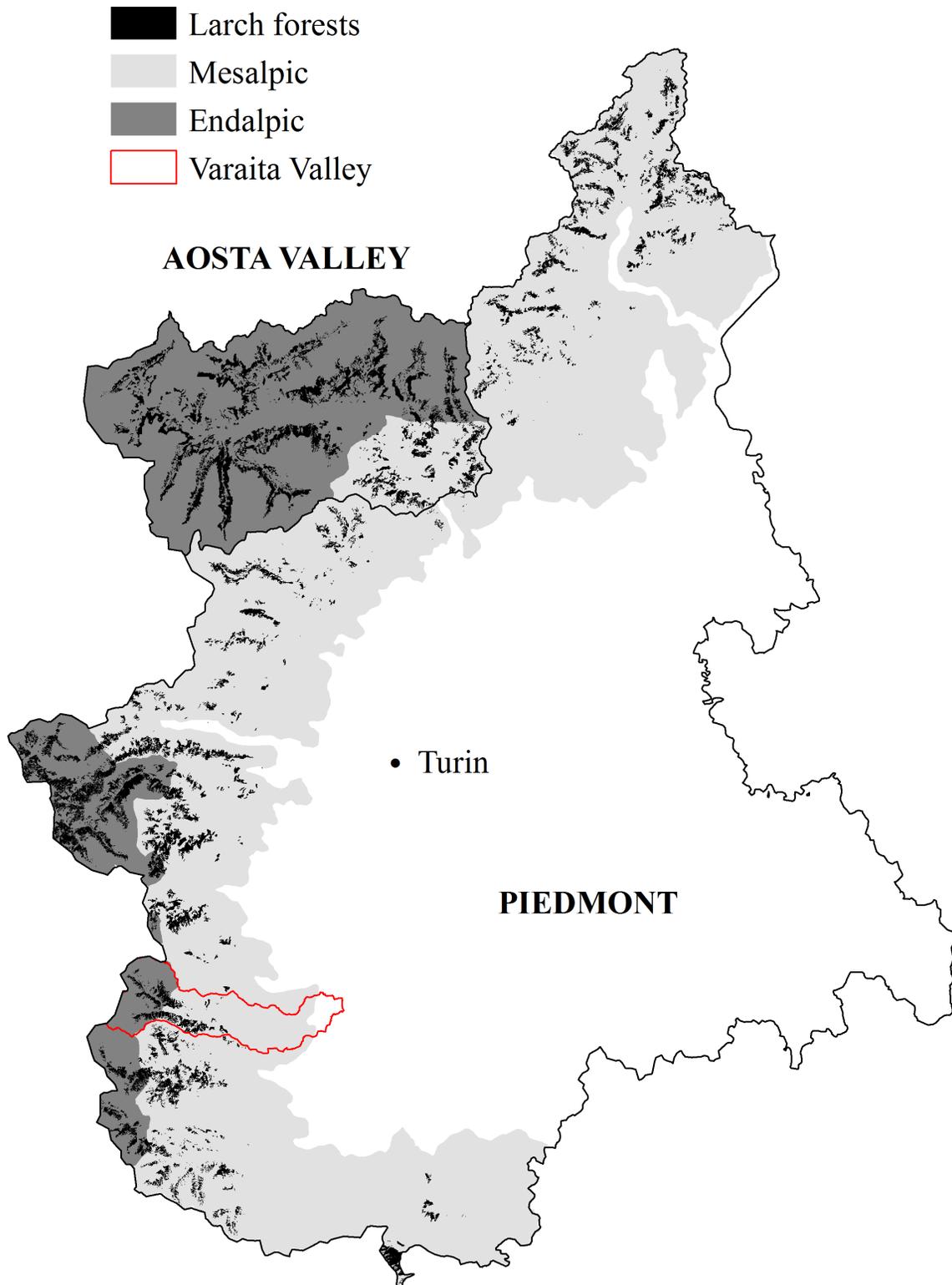


Figure A1. Distribution of larch forests in Piedmont and Aosta Valley. Mesalpic and endalpic climatic sectors in the western Italian Alps. Location of Varaita Valley.

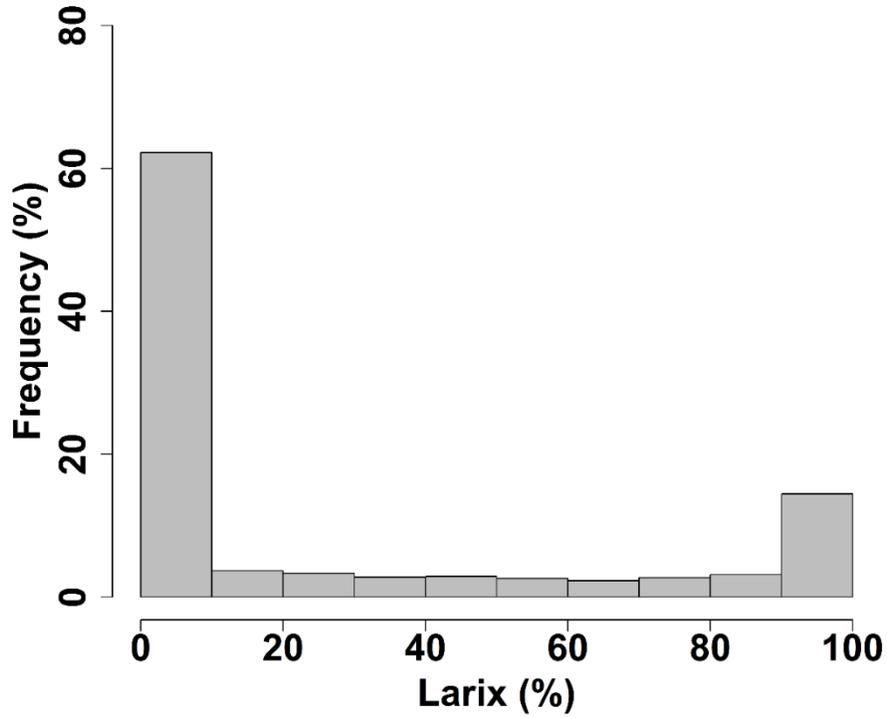


Figure A2. Relative frequency distribution of the state variable.

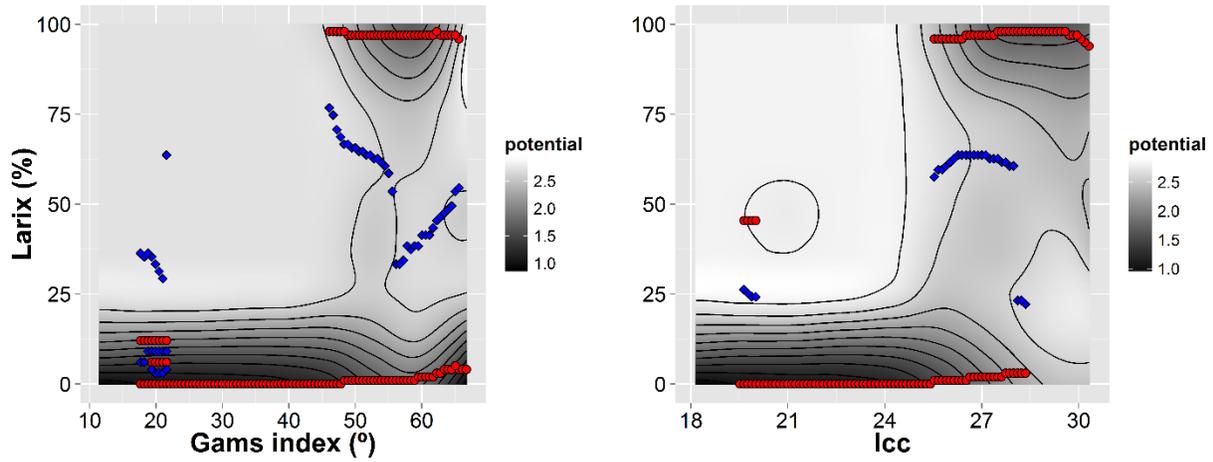


Figure A3. Potential landscape and local minima (red dots) and maxima (blue diamonds) using the state variable (i.e, the percent of larch basal area), and Gams index (left) and lcc (right) as drivers.

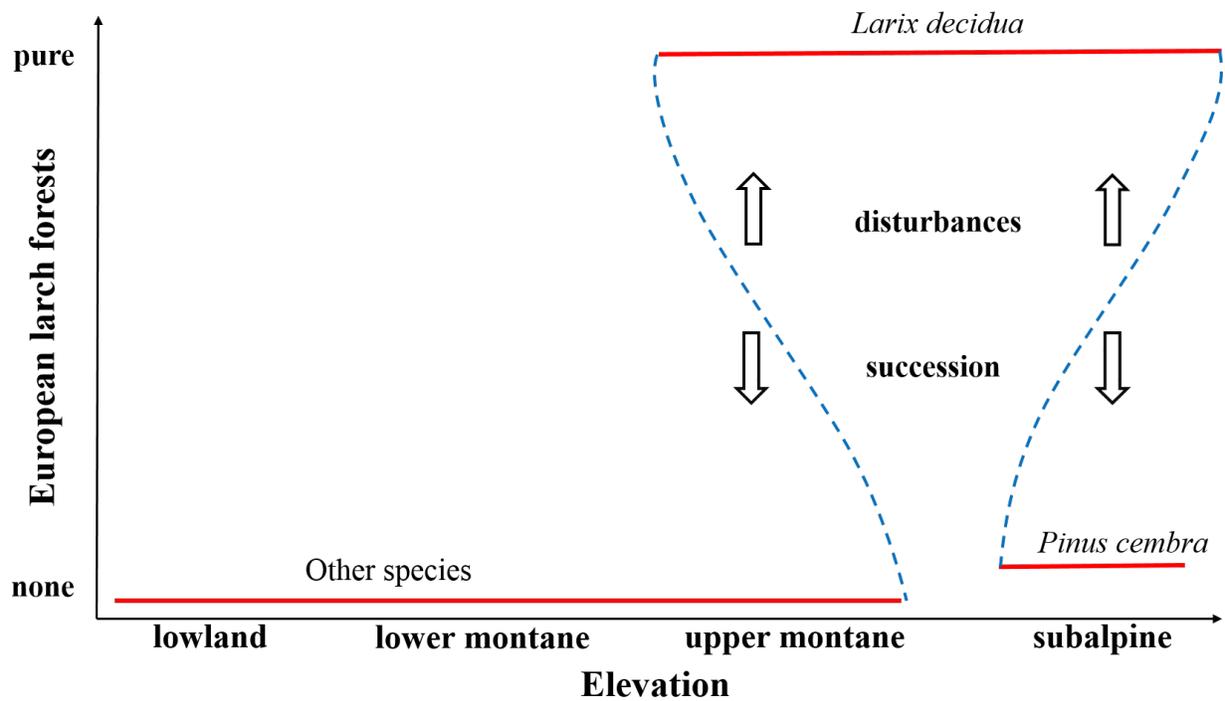


Figure A4. Potential landscape of larch forests in the western Italian Alps. Red straight lines represent stable states and blue dashed lines unstable states. Forest succession changes species composition from pure larch forests to other forest types. Natural disturbances (e.g., forests fires or snow avalanches) and anthropic disturbances (e.g., forest grazing or silvicultural interventions) favor larch regeneration and maintain larch forests. In the subalpine belt, *Pinus cembra* forests are an alternative stable state.



Figure A5. Photos of larch forests in the western Alps. A: European larch forest. B: larch wood pasture. C: mixed *Larix decidua*-*Pinus uncinata* forest. D: regeneration of *Pinus cembra* under *Larix decidua*.