

Using spatial simulations of habitat modification for adaptive management of protected areas: Mediterranean grassland modification by woody plant encroachment

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SUMMARY

Spatial simulation may be used to model the potential effects of current biodiversity approaches on future habitat modification under differing climate change scenarios. To illustrate the approach, spatial simulation models, including landscape-level forest dynamics, were developed for a semi-natural grassland of conservation concern in a southern Italian protected area, which was exposed to woody vegetation encroachment. A forest landscape dynamics simulator (LANDIS-II) under conditions of climate change, current fire and alternative management regimes was used to develop scenario maps. Landscape pattern metrics provided data on fragmentation and habitat quality degradation, and quantified the spatial spread of different tree species within grassland habitats. The models indicated that approximately one-third of the grassland area would be impacted by loss, fragmentation and degradation in the next 150 years. Differing forest management regimes appear to influence the type of encroaching species and the density of encroaching vegetation. Habitat modifications are likely to affect species distribution and interactions, as well as local ecosystem functioning, leading to changes in estimated conservation value. A site-scale conservation strategy based on feasible integrated fire and forest management options is proposed, considering the debate on the effectiveness of protected areas for the conservation of ecosystem services in a changing climate. This needs to be tested through further modelling and scenario analysis, which would benefit from the enhancement of current modelling capabilities of LANDIS-II and from combination with remote sensing technologies, to provide early signals of environmental shifts both within and outside protected areas.

Keywords: adaptation, anthropogenic disturbance, climate change, coupled effects, ecosystem services, land change

scenarios, Mediterranean, protected areas, remote sensing, spatial simulation models

INTRODUCTION

The role of climatic factors in shaping distribution patterns of living organisms is now unquestionable (Woodward & Williams 1987; Huntley *et al.* 1989; Huntley 1999; Hughes 2000; Davis & Shaw 2001; Walther *et al.* 2002; Hamann & Wang 2006). While past and current climates have acted as a major influence on species distribution patterns, early signs of shifts in climate patterns challenge existing approaches to biodiversity conservation that inform laws and policies (Cliquet *et al.* 2009; Heller & Zavaleta 2009).

The current focus on protecting the 'existing values' demonstrated by species associations occurring within protected areas has been critiqued as a rather static approach (Dodd *et al.* 2010). This approach ignores evidence of the individualistic nature of species' response to environmental changes, which is likely to lead to communities that are compositionally unlike those found currently (Brubaker 1981; Williams & Jackson 2007). Furthermore, local natural and anthropogenic disturbances (such as wildfires, grazing, management or land-use change) operate in synergy with global and regional shifts in climate, and play a major role in shaping patterns of vegetation distribution at regional and local scales (Suffling 1995; Forbes 1999; Weber *et al.* 2000; Franklin *et al.* 2001).

Spatially explicit landscape scenarios of potential habitat modification that consider both regional climate change and local disturbances are needed to quantify changes in proxies (for example habitat loss, fragmentation, degradation or biomass) of ecosystem services (such as biodiversity or carbon sequestration) and can help to advance understanding of their effects on current biodiversity conservation approaches, at multiple scales. Scenario maps can be obtained by means of multiscale and multiprocess spatially explicit forest landscape simulation models (Scheller & Mladenoff 2007; Xi *et al.* 2009). These models, considered 'the essence of landscape ecological methods' (Baker 1989, p. 121), can simulate the long-term effects of ecosystem disturbances (for example

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forest harvesting and management, winds, wildfires, pests and diseases), and are suitable to multiple scale applications (Xi *et al.* 2009). Among models adapting stochastic methods and using integrated physical simulation methods to model key ecological processes, material cycles and energy flow (He 2008), the LANDIS model has been used successfully in multiple contexts (He *et al.* 1999; Mladenoff 2004). This grid-based spatially explicit model can be used to simulate landscape-level forest changes, and natural (such as wildfires and windthrow events) and anthropogenic disturbance (for example logging) impacts. LANDIS-II includes variable time steps for different ecological processes, for example woody biomass and carbon dynamics (Sheller & Mladenoff 2007), providing a platform to explicitly incorporate the role of global and regional climate change as a driving force, and to examine their coupled effects with local anthropogenic disturbances.

This study focuses on semi-natural grasslands (EEA [European Environment Agency] 2010), a globally threatened habitat type, and on the Mediterranean region. Grasslands harbour some of the most species-rich plant communities in Europe, hosting a remarkable set of endemic and orchid species (Wilson *et al.* 2012). The Mediterranean region is known for its exceptionally high number (13000) of endemic plants (Myers *et al.* 2000), yet constitutes a threatened conservation region where greater temperature increases, precipitation decreases and extreme events (such as floods, drought and heat waves) are anticipated (IPCC [Intergovernmental Panel on Climate Change] 2007).

The study area was in the Puglia region (southern Italy; Appendix 1, Fig S1, see supplementary material at Journals.cambridge.org/ENC), where agriculture imprints the landscape, forests cover only 9.25% of the land, and scattered non-forest semi-natural habitats, often contiguous or close to forests, occur within a dense network of protected areas. All these vegetation types are either of conservation concern (European Habitats Directive 2007) or protected by law. Local pressures have historically led to loss and fragmentation of grasslands, and climate change is expected to enhance this trend by inducing modifications of other habitat types.

In this study, we aimed to use the outputs of a LANDIS-II application to examine coupled impacts of local pressures and climate change on grasslands in connection with the distribution of tree species. The final goal was to derive suggestions for feasible grassland and forest conservation strategies considering vegetation dynamics at a landscape level, incorporating adaptation (IPCC 2007) into integrated grassland and forest management plans (Splittlehouse 2005; Millar *et al.* 2007; Malmshemer *et al.* 2008; Seppälä *et al.* 2009).

METHODS

Study area

The study area (23800 ha, 16° 30' 5.83"–16° 45' 40.69" W and 40° 48' 13.81"–41° 0' 5.68" N, 380–520 m above

sea level) is representative of the main vegetation types and associated threats of the Natura 2000 (N2K) site of community importance (SCI)/special protection area (SPA) Murgia Alta IT9120007 (European Habitats Directive 2007). The N2K site, also partly designated and managed as a national park (NP), spans over a wide karstic plateau (125 880 ha) surrounded by sedimentary plains under agriculture, and is subject to a Mediterranean macro-bioclimate with a pluviseasonal-oceanic bioclimate, ombrotypes ranging from dry to subhumid, and a meso-Mediterranean thermotype (Forte *et al.* 2005). The N2K site constitutes a training site within the European Union (EU) Seventh Framework Programme (FP7/2007–2013) project BIO_SOS (www.biosos.eu), aimed at developing a pre-operational system for cost- and time-effective monitoring of land cover and habitat changes within and at the fringe of protected areas.

Semi-natural grassland (29800 ha, 24% of the total area), the ecosystem type of main conservation concern at this N2K site, was developed and maintained through a mix of anthropogenic and natural processes, including long periods of grazing by domestic stock, cutting and regimes of deliberate burning. From the 80000 ha that existed at the beginning of the 20th century, by the early 1990s, grassland extent had dropped to 40000 ha, due to transitions to other land uses (largely arable crops). Substantial losses further occurred between 1990 and 2000, mainly due to EU incentives promoting durum wheat production (Appendix 1, Fig S2, see supplementary material at Journals.cambridge.org/ENC) (Boccaccio *et al.* 2013). Pastures have also become prone to woody vegetation encroachment from neighbouring forest vegetation types, after the decline of traditional sheep grazing.

Other sub- and semi-natural vegetation types, some of which are also of conservation concern, include garrigues and scrubs, downy oak (*Quercus pubescens* Willd.) and kermes oak (*Q. coccifera* L.) coppice woodlands and conifer plantations. Forests are subject to an altered (anthropogenic rather than natural) fire regime, directly dependent on human intervention. A forest fire suppression policy is applied throughout the region, and prescribed burning is not in use.

More than one hundred animal species listed in European Directives or other red lists are associated with these vegetation types, which are cast within an agricultural matrix dominated by cereal crops and, to a lesser extent, comprised of olive groves, almond orchards and vineyards (Table 1).

Modelling

The reference LANDIS-II application (Leronni 2013) used for this study included six contrasting scenarios (Table 2), built under specified conditions of climate, tree-growth and dispersal, and disturbance regime, to assess the dynamics of the above ground biomass (AGB) of a set of Mediterranean forest tree species. In the first two scenarios, AGB trends were modelled under both current and projected climatic conditions (NCC_B versus CC_B). Anthropogenic disturbances, namely fires (NCC_B_F versus CC_B_F)

Table 1 Land cover/land use types and habitats of conservation concern in the study area. Sources: ¹Regione Puglia (2008), ² European Habitats Directive (2007) and standard data forms for the ‘Murgia Alta’ IT9120007 SCI/SPA Natura 2000 site.

Land cover/land use type ¹	Area		European Habitats Directive Annex I habitat type ²
	ha	%	
Grasslands	5280	22.2	62A0 Eastern sub-Mediterranean dry grasslands (<i>Scorzoneratalia villosae</i>) 6220* Pseudo-steppe with grasses and annuals of the <i>Thero-Brachypodietea</i> 91AA* Eastern white oak woods
Downy oak woodlands	1910	8.0	
Kermes oak woodlands	94	0.4	
Scrubs	227	1.0	
Conifer plantations	1821	7.7	
Annual crops	7843	33.0	
Permanent crops	5928	24.9	
Developed lands	697	2.9	
Total	23800	100	

Table 2 Scenarios built using LANDIS-II (Leronni 2013).

Extensions	Scenarios	
	No-climate change	Climate change
Biomass succession	NCC_B	CC_B
Biomass succession	NCC_B_F	CC_B_F
Base-fire		
Biomass succession	NCC_B_F_M	CC_B_F_M
Base-fire		
Biomass-harvest		

and management (NCC_B_F_M versus CC_B_F_M), were progressively introduced.

The initial forest structure and composition were derived from a combination of geographic information system (GIS) analysis and data collected in a 2011–2012 field survey of the study area based on stratified random sampling ($n = 53$). Four forest types (coniferous plantations, deciduous/semi-deciduous oak woodlands, evergreen oak woodlands, and shrubs) were identified consisting of 12 stand types (initial communities) with a unique combination of species-age cohorts (Leronni 2013).

Rates of establishment probabilities (SEP) and above ground net primary productivity (ANPP) for five tree species and shrub species, were computed through the ecosystem process model PnET-II (Aber & Federer 1992; Aber *et al.* 1997; Xu *et al.* 2009). The values of the several individual species life-trait and ecophysiological variables were derived from the literature (Baldocchi *et al.* 1988; Ellenberg 1988; Bugmann 1994; Aber *et al.* 1997; Panaiotis *et al.* 1997; Goodale *et al.* 1998; Alifragis *et al.* 2001; Mediavilla & Escudero 2003a, b; Laurent *et al.* 2004; Tapias *et al.* 2004; Wright *et al.* 2004; Niinemets & Valladares 2006; Fyllas *et al.* 2007; Daas *et al.* 2008; Querejeta *et al.* 2008; Paula *et al.* 2009; Xu *et al.* 2009; Xi & Xu 2010), while data relevant to the soil nutrient regime were derived from field surveys ($n = 30$). The study area was treated as a homogeneous ecoregion, based on the main chemical-physical characteristics of the soil and geomorphological features.

Historical monthly averages of climatic variables for the 1960–2010 period were derived from the records of four thermo-pluviometric stations close to the study area.

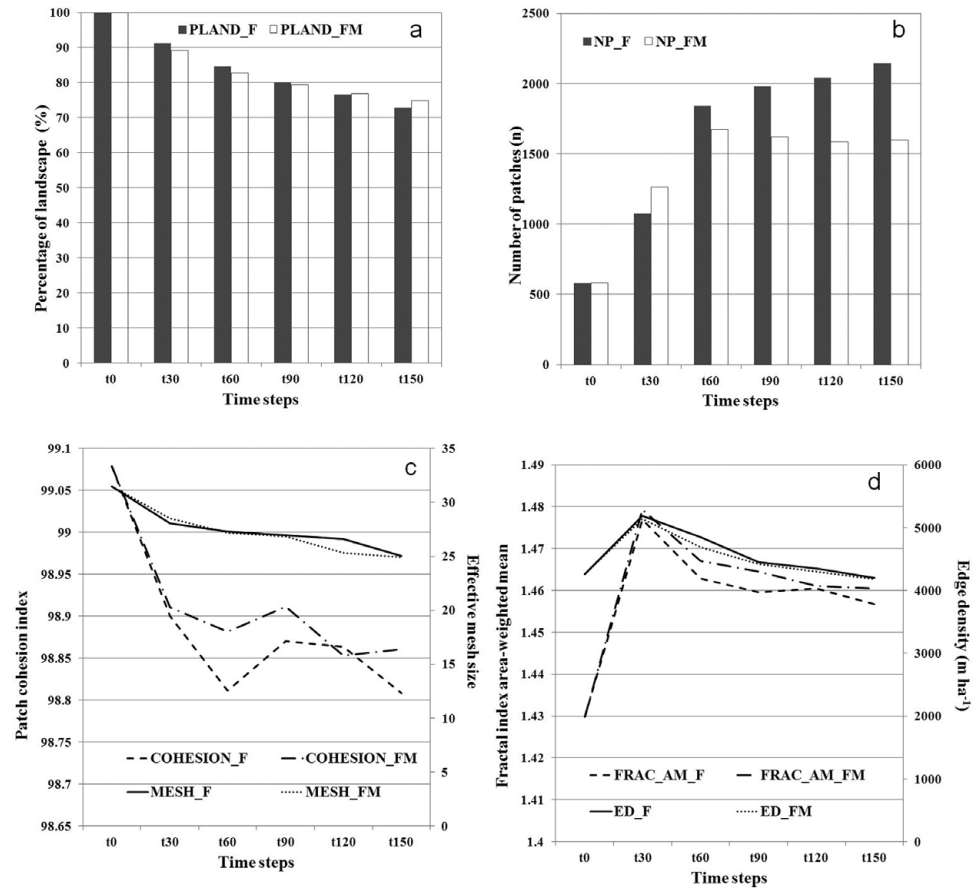
Climate change projections (2010–2060) were derived from the general circulation model GCM ECHAM5 SRES A1B (Roeckner *et al.* 2003), downscaled at RCM (regional circulation model, resolution 0.25°) for the Mediterranean basin (Christensen *et al.* 2009), with atmospheric CO₂ levels stabilizing at c.700 ppm by the year 2100, leading to a 1.6°C increase in mean annual temperature and a 1.3 mm decrease in total annual precipitation for the study area. Photosynthetically active radiation (PAR) intensity was indirectly estimated according to Hargreaves and Samani (1982) and Weiss and Norman (1985). These were extended to 2160, assuming the last time step (2055–2060) of PnET-II outputs were constant for the remaining part of the simulation.

The biomass succession extension was calibrated by comparing model outputs to the real biomass of each initial community, assessed by field survey (Scheller 2012).

The fire disturbance was simulated using the base fire extension (Scheller & Domingo 2012), with the current fire regime specified by a mean observed fire rotation period (FRP) of 75 years, characterizing a moderate fire cycle in other Mediterranean vegetation types (Franklin *et al.* 2001). The calibration was performed through a systematic manual optimization of specified parameters, and comparison between observed average and modelled FRP values (Syphard *et al.* 2007).

The forest management was simulated through the biomass harvest extension (Scheller & Domingo 2013), parameterized to mimic typical harvesting in the region based on forest management prescriptions. A moderate periodical thinning (10–20% biomass, 15 years rotation period) and typical coppicing with release (18–20 years cycle) were applied to coniferous plantations and deciduous oak woods, respectively. The prescription parameter ‘minimum time since damage’ was set to 10 years, according to current regulation, to prevent cutting in areas damaged by fires. Forest management included the elimination of encroaching vegetation on agricultural and other non-forest areas.

Figure 1 Trends in (a) percentage of landscape (PLAND); (b) number of patches (NP); (c) effective mesh size (MESH) and patch cohesion (COHESION); (d) edge density (ED) and fractal index distribution (FRAC_AM) for grasslands. Climate change and wildfires (F), climate change scenario, wildfires and management (FM) scenario.



To assess within-scenario stochasticity, each scenario was replicated three times with a different random seed number. As replications yielded very low variances (2–3%) of response variables, scenario significance testing was not performed, and one replication was selected at random.

From this modelling (Appendix 1, Fig S3, see supplementary material at Journals.cambridge.org/ENC) the two most extreme scenarios (CC_B_F and CC_B_F_M, hereafter and in figures F and FM) were selected for a pairwise quantitative comparison of the spatially explicit dynamics of the biomass of a sub-set of the modelled Mediterranean forest species, namely Aleppo pine (*Pinus halepensis*, Miller), (Ph), downy oak, (Qp) and kermes oak (Qc) within grasslands.

The LANDIS-II output maps for the F and FM scenarios were overlaid in a GIS with a current land-cover/land-use map. Forty quasi-binary biomass (total and individual species) maps (grasslands versus encroachment) at the same grain and extent were obtained for the two scenarios, at five different points in time (year 2030 = t30, 2060 = t60, 2090 = t90, 2120 = t120 and 2150 = t150). These were used to quantify the area and rate of woody encroachment over the next 150 years. The ten total biomass maps were used to compute a set of landscape pattern indices (LPIs) considered suitable to capture the four spatial effects of fragmentation on habitat pattern: reduction in habitat amount, increase in number of habitat patches, decrease in sizes of habitat patches

and increase in isolation of patches (Fahrig 2003). These effects were assessed respectively by means of the percentage of landscape (PLAND), number of patches (NP), effective patch size (MESH) and patch cohesion index (COHESION), computed using FRAGSTATS 3.3 (McGarigal *et al.* 2002). To these, edge density (ED) and fractal index distribution (FRAC_AM) were added to evaluate effects of encroachment on grasslands habitat configuration in terms of the complexity of patch shape and edge length, also related to fragmentation. To explore the relationships between the habitat loss and the configuration components of fragmentation (McGarigal & McComb 1995; Mairota *et al.* 2013) as well as to summarize the set of LPIs, we applied a principal components analysis (PCA).

LANDIS-II output tables were used to quantify encroaching biomass, density of colonizing vegetation (Mg ha^{-1}) and annual average biomass encroaching rates ($\text{Mg ha}^{-1} \text{yr}^{-1}$).

RESULTS

A progressive increase in forest area (from 16% to 35% of the landscape for F scenarios and to 23% of the landscape area for FM scenarios) and a loss to encroachment of almost one-third of grassland habitat (from 22% to 16%) (Fig. 1a; Appendix 1, Fig S4, see supplementary material

Table 3 Summary of the principal components analysis by variable for both the climate change and fire scenario and the climate change, fire and management scenario.

Scenario		PCA components				
		1	2	3	4	5
Climate change and fire scenario	Proportion of total variance	68.84	28.75	1.69	0.71	0.02
	Cumulative proportion	68.84	97.59	99.27	99.98	100.00
	Loadings					
	PLAND_F	-0.935*	-0.342	-0.091	0.023	-0.020
	NP_F	0.947*	0.266	-0.116	-0.139	-0.013
	ED_F	0.020	-0.996*	-0.091	-0.007	-0.001
	FRAC_AM_F	0.669*	-0.721*	0.172	-0.057	0.002
	COHESION_F	-0.969*	0.145	0.184	-0.082	-0.012
	MESH_F	-0.987*	-0.073	-0.090	-0.113	0.020
	Factor scores					
	t0_F	-1.899	0.710	-0.105	0.198	0.068
	t30_F	-0.230	-1.745	0.962	0.374	-0.056
	t60_F	0.341	-0.599	-1.882	0.084	0.379
	t90_F	0.358	0.263	0.044	-1.137	-1.636
	t120_F	0.525	0.482	0.631	-1.065	1.458
t150_F	0.905	0.889	0.350	1.545	-0.214	
Climate change, fire and management scenario	Proportion of total variance	72.05	26.28	1.23	0.44	0.00
	Cumulative proportion	72.05	98.33	99.56	100.00	100.00
	Loadings					
	PLAND_FM	-0.943*	-0.325	0.004	0.069	-0.001
	NP_FM	0.973*	0.018	-0.226	0.034	-0.001
	ED_FM	0.071	-0.997*	0.006	0.033	-0.005
	FRAC_AM_FM	0.773*	-0.627*	0.028	-0.094	0.004
	COHESION_FM	-0.989*	0.041	-0.095	-0.103	-0.007
	MESH_FM	-0.952*	-0.286	-0.113	0.000	0.009
	Factor scores					
	t0_FM	-1.969	0.519	0.051	0.124	-0.042
	t30_FM	-0.053	-1.795	0.876	-0.416	-0.021
	t60_FM	0.370	-0.463	-1.225	1.404	-0.586
	t90_FM	0.333	0.178	-1.242	-1.452	0.612
	t120_FM	0.627	0.636	0.782	0.751	1.481
t150_FM	0.691	0.926	0.758	-0.412	-1.444	

at Journals.cambridge.org/ENC) were observed over the simulation period. No significant differences (*t*-test, $\alpha = 0.05$) were observed between the two scenarios in terms of changes in grassland habitat area nor in the behaviour of the LPIs describing grasslands fragmentation (Fig. 1).

The first two PCA components (PC1, PC2) explaining 98% of the variance were considered for both scenarios (Table 3). PC1 is associated with the LPIs representing the four spatial effects of the process of fragmentation (PLAND, NP, MESH and COHESION), and PC2 with the two ancillary LPIs (ED and FRAC_AM). Increasing fragmentation of the grassland habitat in the landscape at different time steps was indicated by an increase in the degree of the association (PCA scores for cases; Table 3) of such landscapes to PC1 ($r^2 = 0.759$ and $r^2 = 0.669$, respectively, for the two scenarios), with PLAND, MESH and COHESION decreasing and NP increasing. A similar increase in the association between PC2 and both ED and FRAC_AM was only observed from the second time step (t30–t60) onwards, with the values of these two LPIs progressively decreasing. This seems to indicate

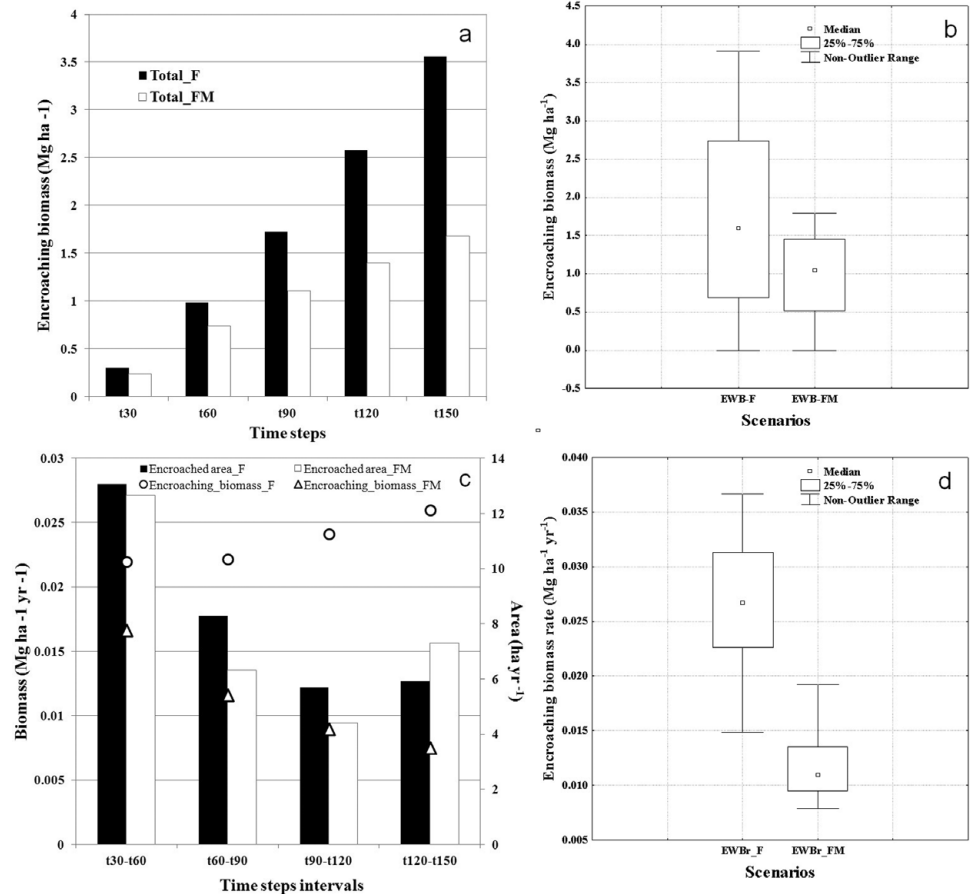
a change in phase (*sensu* Forman 1995 and Jaeger 2000) of the fragmentation process from time step 2 (t30–t60). Thus, the three landscapes where habitat is most fragmented (corresponding to t90, t120 and t150) show higher values of association with both PC1 and PC2.

The densities of encroaching woody biomass were rather low (3.09 Mg ha^{-1} and 1.55 Mg ha^{-1} , respectively, for the two scenarios) but differed (*t*-test, $\alpha = 0.01$) (Fig. 2*a, b*).

Encroachment proceeded at different rates in terms of area in the two scenarios. In both cases a decreasing trend was observed (Fig. 2*c, d*), however the biomass trend was different (*t*-test, $\alpha = 0.01$). The average rate of encroachment of woody biomass increased for the F scenario, while it decreased under the FM scenario, associated with a lower variability in the average rate of biomass encroachment.

Different species showed different colonization trends, amounts and rates of both encroached area and biomass. Moreover, a spatially segregated encroachment by species was observed, and different species varied in spatial encroachment patterns, being either clumped or relatively

Figure 2 (a) Trends and (b) variability in the total amount of woody biomass encroachment per unit area; (c) trends and (d) variability in average annual rates of total amount of woody biomass encroachment and area of woody encroachment in grasslands. F = climate change and wildfires scenario, FM = climate change, wildfires and management scenario.



dispersed (Appendix 1, Fig S5, see supplementary material at Journals.cambridge.org/ENC). This was particularly observed for Ph and Qp.

Overall, the area encroached by these two species was much lower than the area encroached by Qc (Fig. 3a, b). This holds for both scenarios, and is also reflected in the magnitude of the average annual encroachment rates (Fig. 3c, d). The area encroached by Ph decreased with time, and this species was clumped close to the margins of plantations. The area encroached by Qp increased with time, and the species was progressively less clumped, occurring at a relatively greater distance from existing oak coppices. The area encroached by Qc increased with time, and progressively occupied the central part of the study area. Management did not seem to affect the area's average annual encroachment rates for any species.

The contribution of Ph and Qp to encroaching biomass was much lower than that contributed by Qc. This holds for both scenarios, and is also reflected in the magnitude of the average annual encroachment rates (Fig. 4a, b). Management significantly affected encroaching biomass for all species but Ph (Fig. 4c, d), as this tended to be lower in the FM scenario. However, contrasting trends were observed for different species. Ph exhibited a decreasing trend in both scenarios, while Qc depicted a positive trend. Qp showed a more complex pattern of response, decreasing in the F scenario and increasing in the FM scenario. Management seemed also

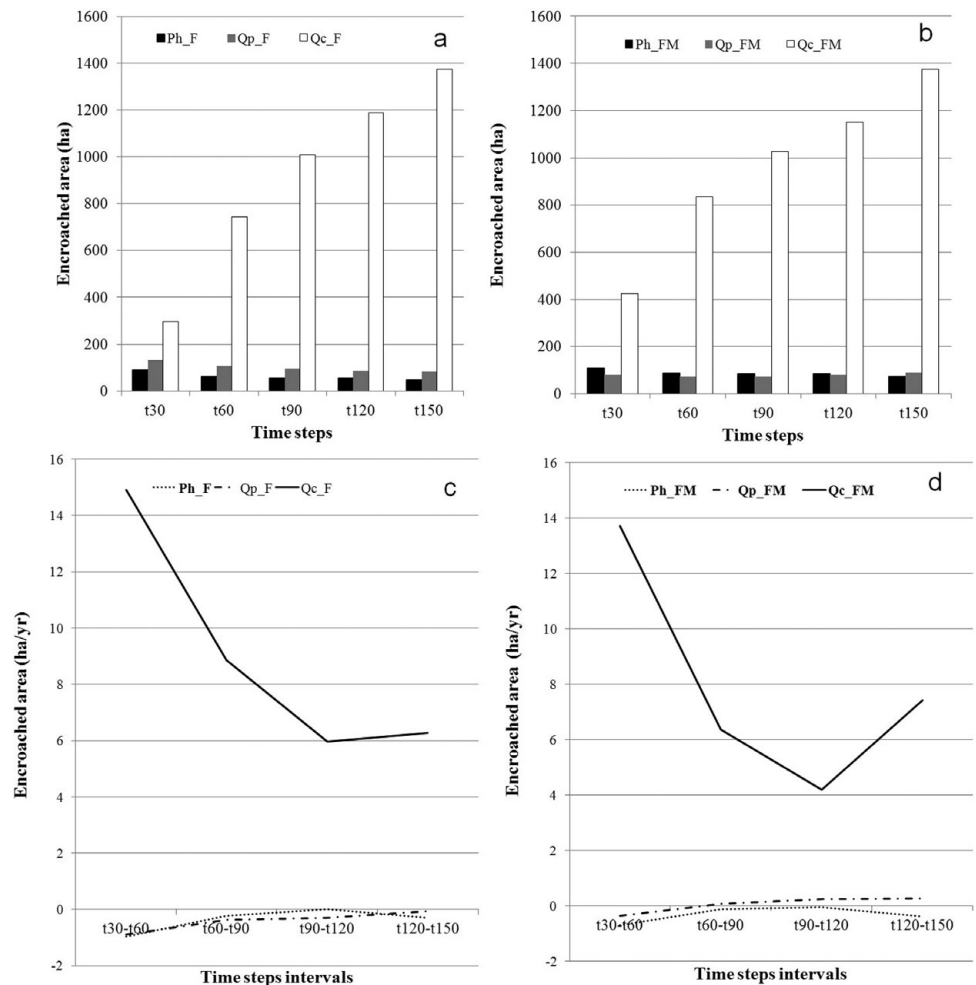
to contrastingly affect biomass average annual encroachment rates (Fig. 4e, f). While no effect was observed in the case of Ph, for Qc and Qp an opposite trend was shown, with the former increasing and the latter decreasing.

DISCUSSION

Woody encroachment into grasslands has constituted an important global threat for this habitat type in many parts of the world over the past 150 years (Chopping *et al.* 2008) altering the capacity of grassland ecosystems to provide essential ecological, hydrological and socioeconomic functions (Hudak & Wessman 1998; Molelele *et al.* 2002; Huxman *et al.* 2005). The simulated changes confirm that, at the local scale, too major impacts might occur at both habitat and landscape levels.

At the habitat level, with regard to biodiversity, close to one-third of the current grassland habitat appears threatened by encroachment. Moreover, as indicated by LPIs, fragmentation of habitat pattern might change in character from an earlier to a later phase (for example, from the dissection to the dissipation phase, *sensu* Jaeger 2000). Simulated changes also indicate that part of the grassland habitat is vulnerable to qualitative changes capable of affecting ecosystem functioning, as changes in plant community structure might lead to scrubby or semi-wooded vegetated habitat types. Modifications in vegetation

Figure 3 Trends in (a, b) overall area of woody encroachment and (c, d) average annual rates of change in area of woody encroachment for selected tree species. Ph = Aleppo pine, Qp = downy oak, Qc = kermes oak. F = climate change and wildfires scenario, FM = climate change, wildfires and management scenario.



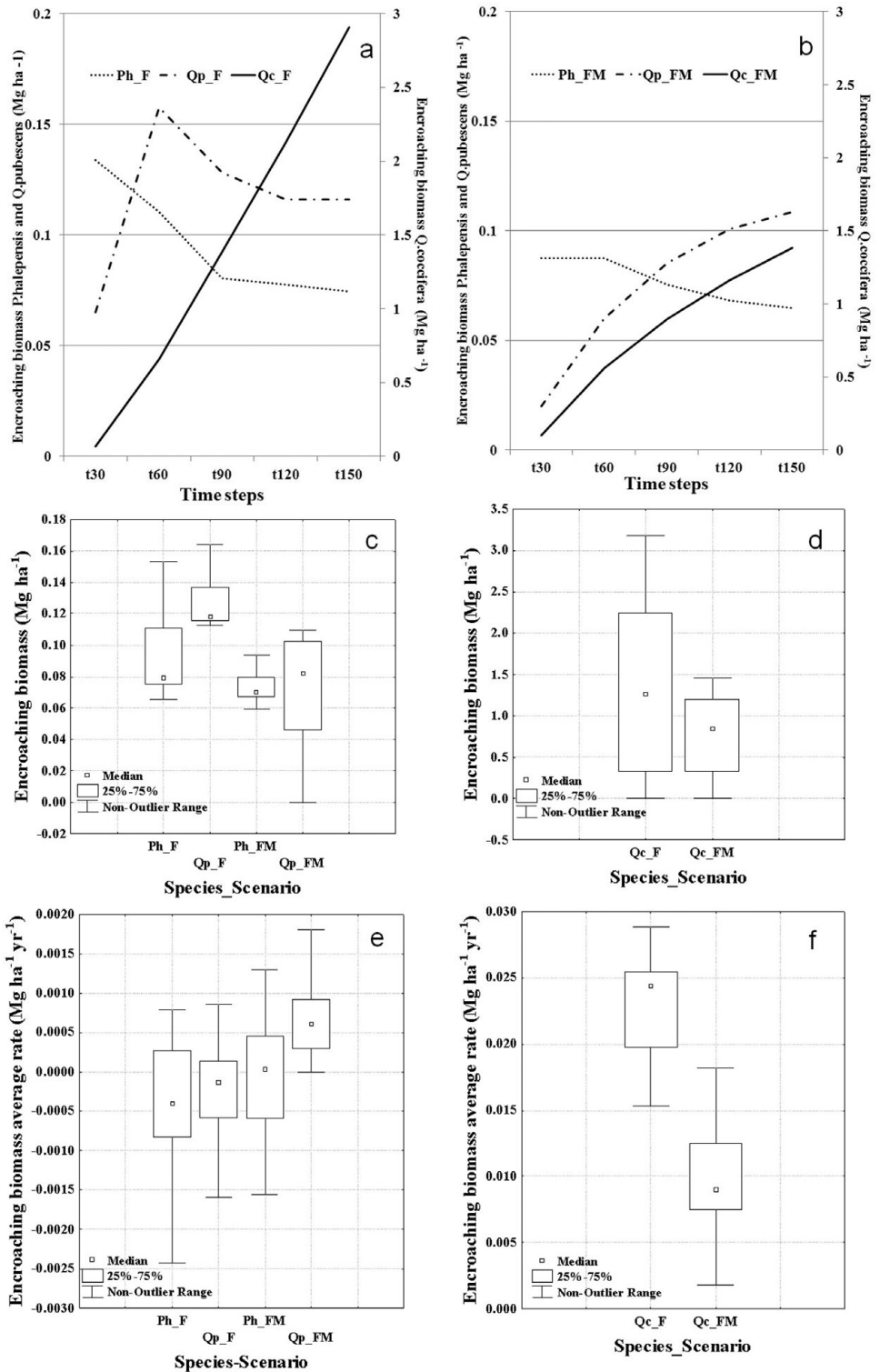
composition and structure due to woody encroachment are likely to determine changes in habitat quality and render it progressively unsuitable to Italian feather (*Stipa austroitalica* Martinovsky), a priority species for conservation, and to a number of other grassland plant species, such as endemic orchids (such as the Apulian spider-orchid, *Ophrys holosericea* subsp. *apulica* [Danesh & Danesh] Buttler). Moreover, grassland habitat deterioration and loss could have cascade effects across food webs at the landscape level, which would impact many animal species that are locally, regionally or globally threatened, including butterflies (such as the Italian marbled white, *Melanargia arge*), grasshoppers (like the spiked magician, *Saga pedo*) and birds (such as the lesser kestrel, *Falco naumanni* and calandra lark, *Melanocorypha calandra*).

Ecosystem level changes (for example carbon sequestration efficiency) might also occur at the habitat level. Grasslands in Europe appear to sequester 3–4 times more carbon in the soil than forests (Ciais *et al.* 2010). Even though losses in soil organic carbon during secondary succession seem to be greater with increasing precipitation (Alberti *et al.* 2011 and literature cited therein), a negative relationship between carbon soil stock and temperature cannot be excluded in areas with a meso-Mediterranean thermotype (*sensu* Rivas-Martínez 2009), although this is contingent on other factors

related to successional phases (such as land-use/cover legacies and litter quality) (La Mantia *et al.* 2013).

At the landscape level, the overall mosaic pattern might be altered progressively as grassland decrease is paralleled by a forest cover increase. This might be possibly associated with compositional changes, as the gradual spread of Qc observed in encroached grasslands at the expense of the other two species could occur in other forests. The decline of Qp was expected, whereas given different life traits, seed dispersal and fire resistance strategies between Qc and Ph, a greater spatial spread and a more intense colonization of the latter could have been envisaged. LANDIS-II might not have been sensitive to sexual maturity, and effective seed dispersal distance as the same values for the two species were derived from the literature (Leronni 2013). However, a competitive advantage might have occurred for Qc because traits and parameters were reported having as higher values than those for Ph, such as fire and shade tolerance. Shade tolerance in particular plays a very important role in both real and LANDIS-II simulated forest succession, as it affects the ability of a tree to reproduce via seeds or resprouting (He & Mladenoff 1999a, b). The probability of Qc establishment also appears to be 1.6 times higher than that of Ph (Leronni 2013). The pattern observed for Qc is compatible with other findings in

Figure 4 Trends in (a, b) biomass of woody encroachment per unit area, (c, d) variability of encroached woody biomass per unit area, and (e, f) variability of average annual rates of encroached woody biomass, for selected tree species. Ph = Aleppo pine, Qp = downy oak, Qc = kermes oak. F = climate change and wildfires scenario, FM = climate change, wildfires and management scenario.



Mediterranean-type ecosystems (Franklin *et al.* 2001; Acácio *et al.* 2009). This is consistent with the life strategies of this species, which appear likely to withstand climate change-induced increases in the intensity and duration of the water stress period. Qc typically concludes twig growth and bud formation between April and May, and it might therefore more successfully escape the drought (and related heat waves) which

strikes particularly around the end of June and beginning of July, when Ph is still growing and pollinating. Qc can also take advantage of a second growth season at the onset of the wet season, when seeds also ripen (Tsiouvaras *et al.* 1987). The decline of Ph, despite its capabilities as an early seeder, could be explained in relation to the fire regime, as there is evidence that many fire-adapted species may be extirpated by

particular fire regimes (Keeley *et al.* 2012). Ph is one such species, and plantations of this species are regarded as fire-sensitive because, due to high fire frequency and incidence of crown fire, they may not be able to recover a sufficient canopy seed bank for population regeneration after fire (Pausas *et al.* 2008).

Thus the question of the effectiveness of the protected area emerges for the conservation of at least two categories of ecosystem services provided by grasslands, biodiversity and carbon sequestration efficiency. The results also bring about other longer-term strategical issues related to the maintenance of the overall landscape arrangement and to the conservation of the currently protected Qp habitat in changing environmental conditions. A growing body of research casts doubts on the capacity of existing protected areas and networks to fulfil conservation objectives grounded on climatic and biogeographic stability in an era of global change, and a range of possible options are being proposed to adapt conservation to such changes (Lemieux & Scott 2005; Hannah 2008; Heller & Zavaleta 2009; Wiens *et al.* 2011). In this study, it seems that a site-scale conservation strategy would be more appropriate than other approaches (such as regional planning and landscape connectivity) considering that biogeographic controls, existing regulatory constraints and socioeconomic conditions hinder the departure from the fixed-boundary protected area strategy. The same constraints indicate that a combined short/middle term (resistance/resilience, *sensu* Millar *et al.* 2007) strategy to vegetation changes might be appropriate to the twofold aim of maintaining grasslands and buffering other landscape level modifications. For the study area, particularly in the context of climate change (Leronni 2013), fire regime appears to be a major driver of change. Current forest management, however, whilst not effective in buffering changes in habitat spatial pattern, significantly influences the degree and the rate of qualitative change in terms of both vegetation composition and structure. Therefore, such local-scale strategies should integrate fire control, improved silviculture and direct encroachment control practices.

Fire prevention in particular might be effective in increasing the fire rotation period. Besides improved patrolling, fire breaks could limit the spread of fire into forests from croplands and grasslands, where burning, however illegal, is traditionally applied during the fire season as a means of soil fertility and pasture improvement. Fire breaks management could be combined with current direct encroachment control practices and the resumption of sheep grazing. Fire prevention silviculture (for example pruning associated with moderate thinning; Notarnicola 2012) could be implemented in older pine plantations, where the primary carrier of crown fires are dead branches accumulated in the lower parts of the canopy. Even though an attenuated fire regime might favour Ph, a non-native species, at the expense of the native oaks as observed, its encroaching spatial potential is limited to the surroundings of plantations. This renders direct control easier. Qp's encroachment potential seems to

be effectively limited by current coppicing. However, this kind of silviculture regime, in the context of climate change, also tends to eliminate Qp from existing woodlands if Qc were to become dominant (Leronni 2013). This does not happen in the F scenario, consistent with the empirical findings of Fabbio *et al.* (2003) who showed higher biomass per unit area in non-managed coppice woodlands, which tended to become fully stocked and multistoreyed. Therefore, the conversion of coppice woodlands to tall forests, at least in higher fertility stands, could balance the need to control encroachment and to enhance the resilience of Qp woodlands in the landscape.

From the perspective of adaptive management, further modelling simulating the alternative management options outlined and the scenario analysis proposed for the assessment of their implications, might greatly aid the design of a feasible strategy to manage environmental change at the local scale (Millar *et al.* 2007; Shang *et al.* 2012). However, such potential is presently hampered in the study area by the lack of biometric data for model parameterization and calibration for the different silvicultural options. Moreover, with reference to the specific case of grassland encroachment, LANDIS-II does not currently allow for the modelling of grass vegetation. Therefore, competition between trees and grasses was not modelled in this study, nor were concurrent changes in grassland species composition caused by the encroachment of woody species. Similarly, other changes that are likely to be induced by climate change could not be evaluated, for example those expected to derive from range shifts of the herbaceous species in the present biotic communities and of other species that might enter and possibly become dominant or invasive species (Bakkenes *et al.* 2002; Martinez-Meyer 2005).

Such complex dynamics represent a challenge for future research. On the one hand, developments of the LANDIS-II model could be aimed at the integration of grassland ecosystem dynamic simulation models (see Thornley 1998) or at exploring the potential for the use of LANDIS-II within the framework of hybrid approaches (Midgley *et al.* 2010), which integrate landscape models and both spatially explicit species distribution models (Elith & Leathwick 2009) and population viability models (Akçakaya *et al.* 2004). On the other hand, LANDIS-II could effectively be used in combination with remote sensing (RS) based landscape change detection technologies, suitable for investigations relevant to grasslands habitat quality (Muldavin *et al.* 2001; Tong *et al.* 2004), especially when combined with spatial modelling (Bradley & Mustard 2006), and with continuous approaches for landscape pattern analysis (Pearson 2002; Hofer *et al.* 2007). Targeted field management actions would also be more effective in minimizing the impact of environmental changes if coupled with RS monitoring aimed at providing early signals of environmental changes (Jump *et al.* 2010). RS data and techniques have proved very useful in helping managers identify early warning signs of climate change at regional (Alcaraz-Segura *et al.* 2009; Silang *et al.* 2010; Altamirano *et al.* 2010) and at local (Lucas *et al.* 2008) scales, as they are

based on early identification of changes in plant physiology and phenology (Nagendra *et al.* 2013). In particular, mapping through RS, including LiDAR (light radar technology), very high spatial resolution datasets and advanced image processing techniques (Nagendra *et al.* 2013), can be extremely important in providing early indication of woody encroachment in grasslands (Chopping *et al.* 2008).

CONCLUSION

Comparative scenario studies are required to facilitate adaptive management, to tackle the combined challenges of climate change and anthropogenic pressure that are being increasingly felt by protected areas across the world (Thompson *et al.* 2012). This study demonstrates that LANDIS-II outputs can be effectively turned into scenario maps of land-cover/land-use useful to assess how human interventions interact with ecological dynamics in complex systems at local scales. These can also support larger-scale spatial modelling and planning (Hannah 2008, Rose & Burton 2009; Wiens *et al.* 2011).

The coupled effects of anthropogenic forcings on an ecological system operate at different spatial scales and seem likely to produce legacy effects at different temporal scales (such as different species biomass encroachment rates), thus adding to the complexity of the dynamics of human-ecological systems. To further understanding of the potential trends of these coupled systems, and to map areas susceptible to future change, current spatially explicit modelling tools capable of handling coupled forcings must be improved and approaches integrating these with RS developed (Liu *et al.* 2007). RS, in particular, would provide a way to map spatial legacies, as well as early warnings of current change (Hudak & Wessman 1998; Chopping *et al.* 2008; Nagendra *et al.* 2013).

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References

- Aber, J.D. & Federer, C.A. (1992) A generalized, lumped-parameter model of photosynthesis, evapotranspiration and net primary production in temperate and boreal forest ecosystems. *Oecologia* **92**: 463–474.
- Aber, J.D., Ollinger, S.V. & Driscoll, C.T. (1997) Modelling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. *Ecological Modelling* **101**: 61–78.
- Acácio, V., Holmgren, M., Rego, F., Moreira, F. & Mohren, G.M.J. (2009) Are drought and wildfires turning Mediterranean cork oak forests into persistent shrublands? *Agroforestry Systems* **76**: 389–400.
- Akçakaya, H.R., Burgman, M.A., Kindvall, O., Wood, C.C., Sjögren-Gulve, P., Hatfield, J.S. & McCarthy, M.A., eds (2004) *Species Conservation and Management. Case Studies*. Oxford, UK: Oxford University Press: 533 pp.
- Alberti, G., Leronni, V., Piazzì, M., Petrella, F., Mairota, P., Peressotti, A., Piussi, P., Valentini, R., Gristina, L., La Mantia, T., Novara, T. & Rühl, J. (2011) Impact of woody encroachment on soil organic carbon and nitrogen in abandoned agricultural lands along a rainfall gradient in Italy. *Regional Environmental Change* **11**: 917–924.
- Alcaraz-Segura, D., Cabello, J., Paruelo, J.M. & Delibes, M. (2009) Use of descriptors of ecosystem functioning for monitoring a national park network: a remote sensing approach. *Environmental Management* **43**: 38–48.
- Alifragis, D., Smiris, P., Maris, F., Kavvadias, V., Konstantinidou, E. & Stamou, N. (2001) The effect of stand age on the accumulation of nutrients in the aboveground components of an Aleppo pine ecosystem. *Forest Ecology and Management* **141**: 259–269.
- Altamirano, A., Field, R., Cayuela, L., Aplin, P., Lara, A. & Rey-Benayas, J.M. (2010) Woody species diversity in temperate Andean forests: the need for new conservation strategies. *Biological Conservation* **143**: 2080–2091.
- Baker, W.L. (1989) A review of models of landscape change. *Landscape Ecology* **2**: 111–133.
- Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R. & Latour, J.B. (2002). Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology* **8**: 390–407.
- Baldocchi, D.D., Hicks, B.B. & Meyers, T.P. (1988) Measuring biosphere-atmosphere exchange of biologically related gases with micrometeorological methods. *Ecology* **69**: 1331–1340.
- Boccaccio, L., Labadessa, R., Leronni, V. & Mairota, P. (2013) Cambiamenti del paesaggio del sito Natura 2000 ‘Murgia Alta’ e frammentazione delle praterie aride = Landscape change in the Natura 2000 ‘Murgia Alta’ site and dry grassland fragmentation (English abstract). In: *IX Congresso nazionale Biodiversità. Atti del convegno. Vol. 3: Territorio, paesaggio e servizi eco-sistemici*, ed. G. Calabrese, C. Pacucci, W. Occhialini & G. Russo, pp. 351–357. Valenzano, Italy: CIHEAM-IAMB [www document]. URL http://www.iamb.it/share/integra_files_lib/files/biodiversita_vol3.pdf
- Bradley, B.A. & Mustard, J. (2006) Characterizing the landscape dynamics of an invasive plant and risk of invasion using remote sensing. *Ecological Applications* **16**: 1132–1147.
- Browning, D.M., Archer, S.R., Asner, G.P., McClaran, M.P. & Wessman, C.A. (2008) Woody plants in grasslands: post-encroachment stand dynamics. *Ecological Applications* **18**: 928–944.
- Brubaker, L.B. (1981) Long-term forest dynamics. In: *Forest Succession. Concepts and Application*, ed. D.C. West, H.H. Shugart & D.B. Botkin, pp. 95–106. New York, USA and Heidelberg and Berlin, Germany: Springer-Verlag.
- Bugmann, H. (1994) On the ecology of mountainous forests in a changing climate: a simulation study. PhD thesis no. 10638.

- Swiss Federal Institute of Technology Zurich, Switzerland: 258 pp.
- Chopping, M., Su, L., Rango, A., Martonchik, J.V., Peters, D.P. & Laliberte, A. (2008) Remote sensing of woody shrub cover in desert grasslands using MISR with a geometric-optical canopy reflectance model. *Remote Sensing of Environment* **112**: 19–34.
- Christensen, J.H., Rummukainen, M. & Lenderink, G. (2009) Formulation of very-high resolution regional climate model ensembles for Europe. In: 2009 ENSEMBLES: Climate change and its impacts: summary of research and results from the ENSEMBLES project, ed. P. van der Linden & J.F.B Mitchell, pp. 47–58. Met Office Hadley Centre, UK.
- Ciais, C., Soussana, J.F., Vuichard, N., Luyssaert, S., Don, A., Janssens, I.A., Piao, S.L., Dechow, R., Lathière, J., Maignan, F., Wattenbach, M., Smith, P., Ammann, C., Freibauer, A., Schulze, E.D. & the CARBOEUROPE Synthesis Team. (2010) The greenhouse gas balance of European grasslands. *Biogeosciences Discuss.* **7**: 5997–6050 [www document]. URL <http://biogeosciences-discuss.net/7/5997/2010/>
- Cliquet, A., Backes, C., Harris, J. & Howsam, P. (2009) Adaptation to climate change. Legal challenges for protected areas. *Utrecht Law Review* **5**: 158–175.
- Daas, C., Montpied, P., Hanchi, B. & Dreyer, E. (2008) Responses of photosynthesis to high temperatures in oak saplings assessed by chlorophyll-a fluorescence: inter-specific diversity and temperature-induced plasticity. *Annals of Forest Science* **65**: 305.
- Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to Quaternary climate change. *Science* **292**: 673–679.
- Dodd, A., Hardiman, A., Jennings, K. & Williams, G. (2010) Protected areas and climate change. Reflections from a practitioner's perspective. *Utrecht Law Review* **6**: 140–1148.
- EEA (2010) The European environment. State and outlook 2010: biodiversity [www document]. URL <http://dx.doi.org/10.2800/6160>
- Elith, J. & Leathwick, J.R. (2009) Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology Evolution and Systematics* **40**: 677–697.
- Ellenberg, H. (1988) *Vegetation Ecology of Central Europe*. Cambridge, UK: Cambridge University Press.
- European Habitats Directive (2007) Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora (consolidated version 1.1.2007) [www document]. URL http://ec.europa.eu/environment/nature/legislation/habitatsdirective/index_en.htm
- Fabbio, G., Merlo, M. & Tosi, V. (2003) Silvicultural management in maintaining biodiversity and resistance of forests in Europe—the Mediterranean region. *Journal of Environmental Management* **67**: 67–76.
- Fahrig, L. (2003) Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* **34**: 487–515.
- Forbes, B.C. (1999) Land use and climate change on the Yamal Peninsula of north-west Siberia: some ecological and socio-economic implications. *Polar Research* **18**: 367–373.
- Forman, R.T.T. (1995) *Land Mosaics*. Cambridge, UK: Cambridge University Press.
- Forte, L., Perrino, E.V. & Terzi, M. (2005). Le praterie a *Stipa austroitalica* Martinsky ssp. *austroitalica* dell'Alta Murgia (Puglia) e della Murgia Materana (Basilicata). *Fitosociologia* **42**: 83–103 (English abstract).
- Franklin, J., Syphard, A.D., Mladenoff, D.J., He, H.S., Simons, D.K., Martin, R.P., Deutschman, D. & O'Leary, J.F. (2001) Simulating the effects of different fire regimes on plant functional groups in Southern California. *Ecological Modelling* **142**: 261–283.
- Fyllas, N.M., Phillips, O.L., Kunin, W.E., Matsinos, Y.G. & Troumbis, A.Y. (2007) Development and parameterization of a general forest gap dynamics simulator for the north-eastern Mediterranean Basin (GREEKFORESTSPECIES). *Ecological Modelling* **204**: 439–456.
- Goodale, C.L., Aber, J.D. & Farrell, E.P. (1998) Predicting the relative sensitivity of forest production in Ireland to site quality and climate change. *Climate Research* **10**: 51–67.
- Hamann, A. & Wang, T. (2006) Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* **87**: 2773–2786.
- Hannah, L. (2008) Protected areas and climate change. *Annals of the New York Academy of Sciences* **1134**: 201–212.
- Hargreaves, G.H. & Samani, Z.A. (1982) Estimating potential evapotranspiration. *Journal of Irrigation and Drainage Engineering* **108**(IR3): 223–230.
- He, H.S. (2008) Forest landscape models: definitions, characterization, and classification. *Forest Ecology and Management* **254**: 484–498.
- He, H.S. & Mladenoff, D.J. (1999a) The effects of seed dispersal on the simulation of long-term forest landscape change. *Ecosystems* **2**: 308–319.
- He, H.S. & Mladenoff, D.J. (1999b) Spatially explicit and stochastic simulation of forest-landscape fire disturbance and succession. *Ecology* **80**: 81–90.
- He, H.S., Mladenoff, D.J. & Crow, T.R. (1999) Linking an ecosystem model and a landscape model to study forest species response to climate warming. *Ecological Modelling* **114**: 213–233.
- Heller, N.E. & Zavaleta, E.S. (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biological Conservation* **142**: 14–32
- Hofer, G., Wagner, H.H., Herzog, F. & Edwards, P.J. (2007) Effects of topographic variability on the scaling of plant species richness in gradient dominated landscapes. *Ecography* **31**: 131–139.
- Hudak, A.T. & Wessman, C.A. (1998) Textural analysis of historical aerial photography to characterize woody plant encroachment in South African savanna. *Remote Sensing of Environment* **66**: 317–330.
- Hughes, L. (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**: 56–61.
- Huntley, B. (1999) Species distribution and environmental change: considerations from the site to the landscape scale. In: *Ecosystem Management: Questions for Science and Society*, ed. E. Maltby, M. Holdgate, M. Acreman & A. Weir, pp. 115–130. Virginia Water, UK: Royal Holloway Institute for Environmental Research.
- Huntley, B., Bartlein, P.J. & Prentice, I.C. (1989) Climatic control of the distribution and abundance of beech (*Fagus L.*) in Europe and North America. *Journal of Biogeography* **16**: 551–560.
- Huxman, T.E., Wilcox, B.P., Breshears, D.D., Scott, R.L., Snyder, K.A., Small, E.E., Hultine, K., William, K.H., Pockman, T. & Jackson, R.B. (2005) Ecohydrological implications of woody plant encroachment. *Ecology* **86**: 308–319.
- IPCC (2007) Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge, UK: Cambridge University Press.

- Jaeger, J.A.G. (2000) Landscape division, splitting index, and effective mesh size: new measures of landscape fragmentation. *Landscape Ecology* 15: 115–130.
- Jump, A.S., Cavin, L. & Hunter, P.D. (2010) Monitoring and managing responses to climate change at the retreating range edge of forest trees. *Journal of Environmental Monitoring* 12: 1791–1798.
- Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G. & Rundel, P.W. (2012) *Fire in Mediterranean Ecosystems: Ecology, Evolution and Management*. Cambridge, UK: Cambridge University Press: 515 pp.
- La Mantia, T., Gristina, L., Rivaldo, E., Pasta, S., Novara, A. & Rühl, J. (2013) The effects of post-pasture woody plant colonization on soil and aboveground litter carbon and nitrogen along a bioclimatic transect. *iForest*: e1–e9 [www document]. URL <http://www.sisef.it/iforest/contents/?id=ifor0811-006>
- Laurent, J.-M., Bar-Hen, A., Francois, L., Ghislain, M. & Cheddadi, R. (2004) Refining vegetation simulation models: from plant functional types to bioclimatic affinity groups of plants. *Journal of Vegetation Science* 15: 739–746.
- Lemieux, C.J. & Scott, D.J. (2005) Climate change, biodiversity conservation and protected area planning in Canada. *The Canadian Geographer* 49: 384–399.
- Leronni, V. (2013) Simulating Mediterranean forest landscape dynamics in the context of climate change., PhD thesis, University of Bari, Bari, Italy.
- Liu, J., Dietz, T., Carpenter, S.R., Folke, C., Alberti, M., Redman, C.L., Schneider, S.H., Ostrom, E., Pell, A.N., Lubchenco, J., Taylor, W.W., Ouyang, Z., Deadman, P., Kratz, T. & Provencher, W. (2007) Coupled human and natural systems. *Ambio* 36: 639–449.
- Lucas, R.M., Bunting, P., Paterson, M. & Chisholm, M. (2008) Classification of Australian forest communities using aerial photography CASI and HyMap Data. *Remote Sensing of Environment* 112: 2088–2103.
- Mairota, P., Cafarelli, B., Boccaccio, L., Leronni, V., Labadessa, R., Kosmidou, V. & Nagendra, H. (2013) Using landscape structure to develop quantitative baselines for protected area monitoring. *Ecological Indicators* 33: 82–95.
- Malmsheimer, R.W., Heffernan, P., Brink, S., Crandall, D., Deneke, F., Galik, C., Gee, E., Helms, J.A., McClure, N., Mortimer, M., Ruddell, S., Smith, M. & Stewart, J. (2008) Potential effects of climate change of forests. *Journal of Forestry* 106: 129–131.
- Martinez-Meyer, E. (2005) Climate change and biodiversity, some considerations in forecasting shifts in species potential distributions. *Biodiversity Informatics* 2: 42–55.
- McGarigal, K. & McComb, W.C. (1995) Relationships between landscape structure and breeding birds in the Oregon Coast Range. *Ecological Monographs* 65: 235–260.
- McGarigal, K., Cushman, S.A., Neel, M.C. & Ene, E. (2002) FRAGSTATS: spatial pattern analysis program for categorical maps. computer software program produced by the authors at the University of Massachusetts, Amherst, USA [www document]. URL <http://www.umass.edu/landeco/research/fragstats/fragstats.html>
- Mediavilla, S. & Escudero, A. (2003a) Photosynthetic capacity, integrated over the lifetime of a leaf, is predicted to be independent of leaf longevity in some tree species. *New Phytologist* 159: 203–211.
- Mediavilla, S. & Escudero, A. (2003b) Relative growth rate of leaf biomass and leaf nitrogen content in several mediterranean woody species. *Plant Ecology* 168: 321–332.
- Midgley, G.F., Davies, I.D., Albert, C.H., Alfwegg, R., Hannah, L., Hughes, G.O., O'Halloran, L.R., Seo, C., Thorne, J.H. & Thuiller, W. (2010) BioMove: an integrated platform simulating the dynamic response of species to environmental change. *Ecography* 33: 612–616.
- Millar, C.I., Stephenson, N.L. & Stephens, S.L. (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications* 17: 2145–2151.
- Mladenoff, D.J. (2004) LANDIS and forest landscape models. *Ecological Modelling* 180: 7–19.
- Moleele, N.M., Ringrose, S., Matheson, W. & Vanderpost, C. (2002) More woody plants? The status of bush encroachment in Botswana's grazing areas. *Journal of Environmental Management* 64: 3–11.
- Muldavin, E.H., Neville, P. & Harper, G. (2001) Indices in grassland biodiversity in the Chihuahuan Desert ecoregion derived from remote sensing. *Conservation Biology* 15: 844–855.
- Myers, N., Mittelmeier, R.A., Mittelmeier, C.G., Da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* 403: 853–858.
- Nagendra, H., Lucas, R.M., Honrado, J.P., Jongman, R.H.G., Tarantino, C., Adamo, M. & Mairota, P. (2013) Remote sensing for conservation monitoring: assessing protected areas, habitat extent, habitat condition, species diversity and threats. *Ecological Indicators* 33: 45–59.
- Niinemets, Ü. & Valladares, F. (2006) Tolerance to shade, drought, and waterlogging of temperate Northern Hemisphere trees and shrubs. *Ecological Monographs* 76: 521–547.
- Notarnicola, G. (2012) Fuel models and canopy properties in Aleppo pine plantations in Puglia for crown fire behaviour modelling. PhD thesis, University of Bari, Bari, Italy (English summary).
- Panaiotis, C., Carcaillet, C. & M'Hamedi, M. (1997) Determination of the natural mortality age of an holm oak (*Quercus ilex* L.) stand in Corsica (Mediterranean Island). *Acta Oecologica* 18: 519–530.
- Paula, S., Arianoutsou, M., Kazanis, D., Tavsanoglu, C., Lloret, F., Buhk, C., Ojeda, F., Luna, B., Moreno, J.M., Rodrigo, A., Espelta, J.M., Palacio, S., Fernández-Santos, B., Fernandes, P. M. & Pausas, J.G. (2009) Fire-related traits for plant species of the Mediterranean Basin. *Ecology* 90: 1420–1420 data file [www document]. URL <http://esapubs.org/archive/ecol/E090/094/default.htm>
- Pausas, J.G., Llovet, J., Rodrigo, A. & Vallejo, R. (2008) Are wildfires a disaster in the Mediterranean basin? A review. *International Journal of Wildland Fires* 17: 713–723.
- Pearson, D.M. (2002) The application of local measures of spatial autocorrelation for describing pattern in north Australian landscapes. *Journal of Environmental Management* 64: 85–95.
- Pizzigalli, C., Palatella, L., Zampieri, M., Lionello, P., Miglietta, M.M. & Paradisi, P. (2012) Dynamical and statistical downscaling of precipitation and temperature in a Mediterranean area. *Italian Journal of Agronomy* 7: 3–12.
- Querejeta, J.I., Barbera, G., Granados, A. & Castillo, V.M. (2008) Afforestation method affects the isotopic composition of planted *Pinus halepensis* in a semiarid region of Spain *Forest Ecology and Management* 254: 56–64.
- Regione, Puglia (2008) Land cover/land use types Regione Puglia official land cover/land use map, 2008 [www document]. URL <http://www.sit.puglia.it/>
- Rivas-Martínez, S. (2009) Worldwide Bioclimatic Classification System, 1996–2009 [www document]. URL <http://www.globalbioclimatics.org>

- Roeckner, E., Bauml, G., Bonventura, L., Brokopf, R., Esch, M., Giorgetta, M., Hagemann, S., Kirchner, I., Kornbluh, L., Manzini, E., Rhodin, A., Schlese, U., Schulzweida, U. & Tompkins, A. (2003) The atmospheric general circulation model ECHAM5. PART I: Model description, Report 349, Max Planck Institute for Meteorology, Hamburg, Germany.
- Rose, N.A. & Burton, P.J. (2009) Using bioclimatic envelopes to identify temporal corridors in support of conservation planning in a changing climate. *Forest Ecology and Management* **258**: 64–74.
- Scheller, R.M. (2012) LANDIS-II Biomass Succession v3.1 Extension UserGuide [www document]. URL <http://www.landis-ii.org/exts/biomass-harvest>
- Scheller, R.M. & Mladenoff, D.J. (2007) An ecological classification of forest landscape simulation models: tools and strategies for understanding broad-scale forested ecosystems. *Landscape Ecology* **22**: 491–505.
- Scheller, R.M. & Domingo, J.B. (2012) LANDIS-II Base Fire v3.0 Extension User Guide [www document]. URL <http://www.landis-ii.org/exts/base-fire>
- Scheller, R.M. & Domingo, J.B. (2013) LANDIS-II Biomass Harvest v2.1 Extension User Guide [www document]. URL <http://www.landis-ii.org/exts/biomass-harvest>
- Seppälä, R., Buck, A. & Katila, P., eds (2009) Adaptation of forests and people to climate change. A global assessment report. IUFRO World Series Volume 22. Helsinki: 224 pp. [www document]. URL www.iufro.org/download/file/4485/4496/Full_Report_pdf/
- Shang, Z., He, H.S., Xi, W., Shifley, S.R. & Palik, B.J. (2012) Integrating LANDIS model and a multi-criteria decision-making approach to evaluate national forest management plan in Missouri Ozarks, USA. *Ecological Modelling* **229**: 50–63.
- Silang, L., Ronggao, L. & Yang, L. (2010) Spatial and temporal variation of global LAI during 1981–2006. *Journal of Geographical Sciences* **20**: 323–332.
- Spittlehouse, D.L. (2005). Integrating climate change adaptation into forest management. *The Forestry Chronicle* **81**: 691–695.
- Stenseth, N.C., Van Horne, B. & Ims, R.A. (1993) Ecological mechanisms and landscape ecology. *Oikos* **66**: 369–380.
- Suffling, R. (1995) Can disturbance determine vegetation distribution during climate warming? A boreal test. *Journal of Biogeography* **22**: 501–508.
- Syphard, A.D., Yang, J., Franklin, J., He, H.S. & Keeley, J.E. (2007) Calibrating a forest landscape model to simulate frequent fire in Mediterranean-type shrublands. *Environmental Modelling & Software* **22**: 1641–1653.
- Tapias, R., Climent, J., Pardos, J.A. & Gil, L. (2004) Life histories of Mediterranean pines. *Plant Ecology* **171**: 53–68.
- Thompson, J.R., Wiek, A., Swanson, F.J., Carpenter, S.R., Fresco, N., Hollingsworth, T. & Foster, D.R. (2012) Scenario studies as a synthetic and integrative research activity for long-term ecological research. *BioScience* **62**: 367–376.
- Thornley, J.H.M. (1998) *Grassland Dynamics: An Ecosystem Simulation Model*. Wallingford, UK and New York, NY, USA: CAB International: 241 pp.
- Tong, C., Wu, J., Yong, S., Yang, J. & Yong, W. (2004) A landscape-scale assessment of steppe degradation in the Xilin River Basin, Inner Mongolia, China. *Journal of Arid Environments* **59**: 133–149.
- Tsiouvaras, C.N. (1987) Ecology and management of kermes oak (*Quercus coccifera* L.) shrublands in Greece: a review. *Journal of Range Management* **40**: 542–546.
- Walther, G.-R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.-M., Hoeg-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature* **416**: 389–395.
- Weber, G.E., Moloney, K. & Jeltsch, F. (2000) Simulated long-term vegetation response to alternative stocking strategies in savanna rangelands. *Plant Ecology* **150**: 77–96.
- Weiss, A. & Norman, J.M. (1985) Partitioning solar radiation into direct and diffuse, visible and near-infrared components. *Agricultural and Forest Meteorology* **34**: 205–213.
- Wiens, J.A., Seavy, N.E. & Jongsomjit, D. (2011) Protected areas in climate space: what will the future bring? *Biological Conservation* **144**: 2119–2125.
- Williams, J.W. & Jackson, S.T. (2007) Novel climates, no-analog communities, and ecological surprises. *Frontiers in Ecology and the Environment* **5**: 475–482.
- Wilson, J.B., Peet, R.K., Dengler, J. & Pärtel, M. (2012) Plant species richness: the world records. *Journal of Vegetation Science* **23**: 796–802.
- Woodward, F.I. & Williams, B.G. (1987) Climate and plant distribution at global and local scales. *Vegetatio* **69**: 189–197.
- Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.L., Niinemets, Ü., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.J., Veneklaas, E.J. & Villar, R. (2004) The worldwide leaf economics spectrum. *Nature* **428**: 821–827.
- Xi, W. & Xu, C. (2010) PnET-II for LANDIS-II 5.1 User Guide [www document]. URL <http://www.landis-ii.org/users/PnETforLANDIS-IIUserGuide-V1.0.pdf>
- Xi, W., Coulson, R.N., Birt, A.G., Shang, Z.-B., Waldron, J.D., Charles, W., Lafon, C.W., Cairns, D.M., Tchakerian, M.D. & Klepzig, K.D. (2009) Review of forest landscape models: types, methods, development and applications. *Acta Ecologica Sinica* **29**: 69–78.
- Xu, C., Gertner, G. Z. & Scheller, R. M. (2009) Uncertainties in the response of a forest landscape to global climate change. *Global Change Biology* **15**: 116–131.