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MANAGING FOREST LANDSCAPES UNDER GLOBAL CHANGES: SIMULATION MODELS FOR SCENARIO EVALUATION

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DEDICATION

To those who have yet to arrive.

A aquells que encara han d'arribar.

PREFACE

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TABLE OF CONTENTS

PREFACE vi

LIST OF FIGURES x

LIST OF TABLES xiv

RÉSUMÉ xvii

ABSTRACT xxi

INTRODUCTION 1

CHAPTER I
A SPATIAL ALLOCATION PROCEDURE TO MODEL LAND-USE/LAND-COVER CHANGES: ACCOUNTING FOR OCCURENCE AND SPREADING PROCESSES 13

1.1 Abstract 15

1.2 Introduction 16

1.3 Methods 21

1.3.1 The spatial demand-allocation procedure 21

1.3.2 Sensitivity analysis of the demand-allocation procedure 27

1.3.3 Modelling LULC changes in a Mediterranean region using a spatially explicit demand-allocation LULC change model 29

1.4 Results 35

1.4.1 Sensitivity analysis of the demand-allocation procedure 35

1.4.2 Modelling LULC changes in a Mediterranean region 41

1.5 Discussion 49

1.5.1 Strengths and limitations of the spatially demand-allocation procedure .. 49
1.5.2 Comparison with other demand-allocation approaches 52
1.5.3 Future land-use change scenarios 55
1.6 Conclusions 56
1.7 Acknowledgments 57
CHAPTER II
THE POTENTIAL OF AGRICULTURAL CONVERSION TO SHAPE FOREST FIRE REGIMES IN FIRE-PRONE LANDSCAPES 58
2.1 Abstract 60
2.2 Introduction 61
2.3 Methods 67
2.3.1 Study area 67
2.3.2 The MEDFIRE, a fire-succession model 68
2.3.3 The MEDLUC, a land-use land-cover change model 70
2.3.4 Coupling fire-succession and land-use change models 70
2.3.5 A fire succession strategy sensitive to landscape configuration 72
2.3.6 Landscape management scenarios 75
2.3.7 Analysis of scenarios 77
2.4 Results 80
2.5 Discussion 91
2.5.1 A meta-model for fire-prone landscapes integrating natural and anthropogenic drivers of change 93
2.5.2 Implications for managing fire-prone landscapes in view of global change 94
2.6 Acknowledgments 97
CHAPTER III
ENHANCING FOREST RESILIENCE TO GLOBAL CHANGE: MANAGING TREE FUNCTIONAL DIVERSITY AND CONNECTIVITY IN FRAGMENTED LANDSCAPES 98
3.1 Abstract 100

3.2 Introduction 101
3.3 Methods 106
3.3.1 Study area and sampling design 106
3.3.2 Functional network 107
3.3.3 Measures for the five resilience related properties 113
3.3.4 Simulation of management strategies and forest disturbances 114
3.3.5 Comparing landscapes 117
3.4 Results 118
3.4.1 The reference network 118
3.4.2 Forest disturbances in the reference network 121
3.4.3 Response of the simulated landscapes to disturbances 123
3.5 Discussion 129
3.5.1 Limitations and further research 131
3.6 Acknowledgments 133
CONCLUSION 134
ANNEX A
CALIBRATION METHODOLOGY - CHAPTER 1 147
ANNEX B
COMPLEMENTARY RESULTS - CHAPTER 1 150
ANNEX C
STUDY REGION: CATALONIA - CHAPTER 2 155
ANNEX D
INITIALIZATION OF MEDFIRE AND MEDLUC MODELS - CHAPTER 2 164
ANNEX E
COMPLEMENTARY RESULTS - CHAPTER 2 178
ANNEX F
ADDITIONAL DETAILS OF METHODS - CHAPTER 3 187
ANNEX G
COMPLEMENTARY RESULTS - CHAPTER 3 196
REFERENCES 203

LIST OF FIGURES

Figure 1.1 Flow diagram of the spatial procedure that uses an ascending-order queue of pixels susceptible to undergone change to allocate the demand of a land-cover transition (black squared boxes). The demand-allocation procedure is embedded in MEDLUC model's working diagram (grey boxes are all user-defined) 25

Figure 1.2 2009 Land Cover Map of Catalonia (32 100 km^2) reclassified to four categories: urban in red, natural vegetation in green, agricultural land in yellow, and others in grey (a); zoom in for the land transitions observed between 1993 and 2009 in the northeastern part of Catalonia at 1 ha (b); and a situation map of Catalonia in the European context (c) 33

Figure 1.3 Contour plots of the estimated exponent of the power-law distribution (*beta*), the proportional number of patches to allocate a 100-pixel demand (*nptch*), the mean patch size (*mn.size*), the maximum patch size (*mx.size*), and the maxim fractal dimension index (*mx.frac*) as a function of the model parameters λ_i (rate of land-use change origination) and λ_s (rate of land-use change contagion). In each column (from left to right) the model parameter k (intensity of contagion) takes value 0.1, 0.3, and 0.5 respectively 38

Figure 1.4 Patches of change generated by the demand-allocation procedure. One replicate for each of the nine selected scenarios is plotted. For these scenarios the $\{\lambda_i, \lambda_s, k\}$ parameters are A1 : {20, 0.1, 0.1}; B1 : {20, 0.1, 0.3}; C1 : {20, 0.1, 0.5}; A2 : {20, 10, 0.1}; B2 : {20, 10, 0.3}; C2 : {20, 10, 0.5}; A3 : {0.25, 10, 0.1}; B3 : {0.25, 10, 0.3}; C3 : {0.25, 10, 0.5} respectively. For each replica are given the estimated exponent of the power-law distribution (b), the proportional number of patches to allocate a 100-pixel demand (*nptch*), the mean patch size (*mn.size*), the maximum patch size (*mx.size*), and the maxim fractal dimension index (*mx.frac*). Plots size is 180 km^2 and spatial resolution is 1 km 40

Figure 1.5 Probability density functions in a log-log scale for the patches-of-change size distributions at 1 km^2 and at 1 ha of spatial resolution for the three main land-use/cover transitions occurred in Catalonia from 1993 to 2009. Each panel shows the empirical probability density (empty black dots) and the distribution of the maximum likelihood experiment simulated by MEDLUC (full grey dots) 47

Figure 1.6 Percentage correct for three dynamic land-cover types (urban, natural and semi-natural lands, and agriculture) given by the Null model: the 1993 and 2009 versions of the Land Cover Map of Catalonia are cell-by-cell compared at 1 ha and at multiple coarser resolutions. The mean percentages correct of the MEDLUC model correspond to the maximum likelihood scenario initially run at 1 ha and further generalized at multiple coarser resolutions. The mean percentages are averaged over 50 runs ... 48

Figure 2.1 Two contrasting hypotheses about the non-linear relations between fire suppression effectiveness and the amount of agriculture allocated in the landscape (i.e. demand). Horizontal line is at 0.5 of effectiveness while the vertical line indicates the demand leading at 0.5 of effectiveness ... 66

Figure 2.2 Two wind-driven fires (A and C) and one convective fire (B) suppressed at high and low levels of suppression (*Th* = 5 and 15 ha, respectively). For each fire, the upper panel shows the land-cover types: (1) non burnt (crop - yellow, green - forest, brown - shrub, grey - urban in pastel), (2) burnt (same colour code but darker), and (3) suppressed (same colour code but even darker). The lower left panel shows the total burnt (black) and suppressed (light grey) area with the ignition point (dark grey). The lower right panel shows the progression of the fire front (from light grey to black). Spatial resolution is 1 ha. The length of plots A and B is 100 cells, and plot C is 40 cells. The value in the lower left panel indicates the percentage of suppressed area. Fire suppression is barely activated in the 3000 ha wind-driven fire (A) at both thresholds because fire front advances in high intensity across scrublands and forest, burning them. The convective fire (B) is completely suppressed when *Th* is 5 ha (because the ignition point is located in the middle of an agricultural patch) but when the suppression is weaker (Th = 15 ha), the suppressed area is reduced to 63%. The 500 ha wind-driven fire (C) clearly benefits from the agricultural area impeding the fire advance 73

Figure 2.3 Initial transition-potential map (year 2010) for the Fire Management (A), Rural Development (B), and Crop Production (C) storyline 76

Figure 2.4 Relationship between (a) effectiveness, (b) leverage, (c) forest patches mean core area, and (d) forest patches mean shape index at different agricultural demands (50, 100, 200, and 300 $km^2 \cdot year^{-1}$ are D2, D, 2D, and 3D respectively), according to the strategy (Forest Management, FM; Rural Development, RD; and Crop Productivity, CP) and the spatial pattern of new agricultural patches (aggregate vs. scattered). Response variables are measured over the last 20 years of the simulated period. Solid black line in panel (a) indicates effectiveness of the control scenario with only urbanization, while in panels (c) and (d) it indicates the metric value of the reference year 2010 81

Figure 2.5 Cumulative effect of agricultural conversion on fire suppression effectiveness for each of the 24 landscape scenarios (3 strategies, 2 types of aggregation, and 4 levels of demand) from 2016 to 2050 inclusively 82

Figure 2.6 Proportional increase (triangles that point upwards) or decrease (triangles that point downwards) of the forest patches mean core area in the 7 *vegueries* (administrative - biogeographic division of Catalonia) as agricultural demand increases from D2 = 50, D = 100, 2D = 200, to 3D = 300 $km^2 \cdot year^{-1}$ (for the Rural Development strategy and the aggregate pattern of allocation). Grey background accounts for the standard deviation of the metric (that increase as grey become darker) 90

Figure 3.1 Land-cover map of the Central Québec region with seven landscape elements at 1 ha spatial resolution (units on the x-axis and y-axis are in km) 110

Figure 3.2 Functional network representing the reference landscape. Node's size is proportional to the betweenness centrality index BC^{PC} and node's colour varies along functional diversity index *FDis*. The BC^{PC} index of a node measures the number of shortest paths between each pair of nodes that pass through that target node. Nodes with high BC^{PC} values are those that control most of the network flow and constitute the backbone of the forest network 111

Figure 3.3 Species accumulation curves for deciduous and mixed forest patch types 112

Figure 3.4 Log response ratio of response diversity (A), functional redundancy (B), connectivity (C), modularity (D), and mean generalized betweenness centrality index (E) between the 33 managed networks and the reference network 120

Figure 3.5 The five resilience associated properties for the functional network of forest patches of the reference landscape, and once it was disturbed by drought, pest and harvest episodes 122

Figure 3.6 The five resilience associated properties: response diversity *RD*, functional redundancy *FR*, connectivity *PC*, modularity *Q*, and mean generalized betweenness centrality index BC^{PC} for the functionally enriched (A, C, and E) and the planted landscapes (B, D, and F) affected by drought (A and B), pest outbreak (C and D), and timber harvesting (E and F). The selected species were drought tolerant, pest resistant, and biodiversity enhancer for the simulated landscapes affected by drought (A and B), pest outbreak (C and D), and timber harvesting (E and F), respectively. In all radar plots the reference network has also been affected by the corresponding disturbance 127

LIST OF TABLES

Table 1.1 Observed land-cover change demands in Catalonia from 1993 to 2009 for the three land transitions, at 1 km^2 and 1 ha of spatial resolution derived from the Land Cover Maps of Catalonia 32

Table 1.2 Estimates and F-values of the log-log regressions between the allocation parameters (and the two by two respective interactions) and the metrics characterizing patches-of-change distributions: the estimated slope of a power-law distribution (β), the number of patches per total demand (*nptch.dmnd*), the mean patch size (*mean.size*), the maximum patch size (*max.size)*, and the maximum fractal dimension index (*max.frac.dim*) ... 37

Table 1.3 Power-law exponent β_{obs} of the patches-of-change size distribution of the three main land-cover transitions observed in Catalonia between 1993 and 2009, at 1 km^2 and 1 ha of spatial resolution. Probability density functions were logarithmically transformed, and adjusted R^2 is for the slope parameter β_{obs} fitted by linear regression. For each land-cover transition, are provided the relative number of patches to allocate a 100-pixels demand (*nptch.dmnd*), the mean patch size and the standard deviation in brackets (*ptch.size*), the maximum patch size (*max.size*), the mean fractal dimension index and the standard deviation in brackets (*frac.dim*), and the maximum fractal dimension index (*max.frac*) 44

Table 1.4 Calibration results for the three land-cover transitions modeled in Catalonia between 1993 and 2009 at 1 km^2 and 1 ha. The set of parameters {λ_i, λ_s, k} is given for the experiment that generates the patches-of-change distribution that in average minimize the difference between the estimated and the observed probability density functions. For these experiments are given the estimated power law β_{est} parameter for the mean probability density function of the patches-of-change size distribution, the relative number of patches to allocate a 100-pixels demand (*nptch.dmnd*), the mean patch size (*mean.size*), the maximum patch size (*max.size*), and the mean fractal dimension index (*mean.frac.dim*). Metrics are averaged over the 20 model's replicas except for the maximum patch size metric that the median is assessed 45

Table 1.5 Percentage of cells correctly classified as urban, natural and semi-natural vegetation, agricultural land, and other land-cover types (water bodies and bare soil) by the null model and the MEDLUC model at 1 km^2 and 1 ha spatial resolution 46

Table 2.1 Identification codes for the 24 landscape management scenarios that identify the strategy, the level of demand, and the spatial pattern for new agricultural land 79

Table 2.2 Number of years required for a statistically significant improvement on fire suppression effectiveness for each scenario with respect to the effectiveness of the 2016-2020 period. Average number of years for improvement of the scenarios at the same demand level (μ_6), of the scenarios at low vs. high demands (μ_{12}), and of all the scenarios (μ_{24}). Blank value means there were no statistically significant improvement over all the period. Acronyms D2, D, 2D, and 3D stand for the level of agriculture conversion demand in scenarios: 50, 100, 200, and 300 km^2·year^{-1}, respectively.. 83

Table 2.3 Analysis-of-variance (type II tests) of the interaction between the quantitative variable (quantity of agriculture conversion; *demand*) and the categorical variable (*strategy*) on effectiveness of the scenarios when using an aggregate pattern 86

Table 2.4 Coefficients and significance of the linear model $effectiveness|_{\text{aggregate\_pattern}} = f\,(demand, strategy)$ 87

Table 2.5 Analysis-of-variance (type II tests) of the interaction between the quantitative variable (*demand*) and the categorical variable (*strategy*) on effectiveness of the different strategies when using a scattered pattern 88

Table 2.6 Coefficients and significance of the linear model *effectiveness*$|_{\text{scattered\_pattern}}$ $= f(demand, strategy)$ 89

Table 3.1 Code for the 11 management strategies identifying the amount of area to be managed and the type of target patch to be functionally enriched or the type of plantation 116

Table 3.2 Percentage of trees killed by a simulated drought and a pest outbreak in the reference landscape and in the 33 managed landscapes (combining two management strategies (Table 3.1) and a three species functional trait selection criterion, B stands for the biodiversity enhancer, D stands for the drought tolerant, and P stands for the pest resistant, respectively). Differences between the drought- and pest-induced mortality for each of the 33 managed landscapes are also shown 124

RÉSUMÉ

Les paysages forestiers intensivement aménagés sont des systèmes socio-écologiques complexes exposés à de multiples facteurs de changement. Leur dynamique résulte de plusieurs interactions qui agissent à multi-échelles entre les processus écologiques, les régimes de perturbations naturelles, les activités anthropiques et les facteurs exogènes tels que le climat. Les changements globaux devraient interférer sur ces processus conduisant à une réduction de la résilience des paysages forestiers (c'est-à-dire la capacité de faire face et de s'adapter aux pressions exogènes et aux perturbations) à diverses perturbations simples ou cumulatives. De nouvelles stratégies d'aménagement forestier adaptées aux conditions environnementales futures doivent être développées et étudiées.

Dans cette thèse, je présente deux approches de modélisation par simulation pour caractériser les écosystèmes forestiers afin d'évaluer ensuite des stratégies d'aménagement forestier à l'échelle du paysage afin de les appliquer dans un contexte d'incertitude causée par les changements globaux. Toutes les stratégies proposées visent à améliorer la résilience des paysages forestiers aux changements des régimes de perturbations. J'applique chacune de ces deux approches de modélisation à deux régions forestières ayant des degrés d'aménagement distincts. Premièrement, j'explore une politique de réduction du combustible à l'échelle de paysage qui vise à influencer le régime de feu d'un paysage méditerranéen européen vulnérable aux

incendies en utilisant un méta-modèle dynamique du paysage. J'ai développé un modèle spatialement explicite de changements d'utilisation du territoire qui est ensuite couplé à un modèle de dynamique feu-végétation spatialement explicite déjà existant. Cette approche de méta-modélisation a été utile pour étudier la variabilité de l'efficacité de la suppression du feu due à la conversion agricole. Les terres agricoles (sites avec faible disponibilité de combustible qui réduissent l'intensité du feu et permet aux pompiers de se rapprocher des fronts d'incendie) ont été réparties dans le paysage à divers taux annuels, selon un schéma spatial dispersé ou agrégé, et selon trois scénarios illustrant la gestion potentielle des incendies dans la région. Deuxièmement, je cherchais à comprendre si l'amélioration de la diversité fonctionnelle ou de la connectivité d'un paysage agro-forestier fragmenté dans le sud-est du Canada favorise la résilience des écosystèmes aux perturbations naturelles et anthropiques. Ici, j'ai introduit une évaluation multi-échelle de la résilience de la forêt basée sur les traits fonctionnels de réponse des espèces et des propriétés du réseau spatial. J'ai testé l'approche pour déterminer si des stratégies de gestion alternatives peuvent prévenir les diminutions de la résilience selon plusieurs scénarios futurs de sécheresse, épidémie, et récolte forestière.

Dans le paysage méditerranéen vulnérable aux incendies, j'ai découvert une relation non linéaire entre la quantité de nouvelles terres agricoles allouées dans le paysage et l'efficacité de la suppression des incendies. L'efficacité de suppression des incendies n'a guère augmenté à des taux de conversion annuels à terres agricoles faibles / modérés, mais elle a fortement augmenté à des taux de conversion annuels élevés, ce qui signifie qu'il faut atteindre un certain seuil avant que le système ne devienne plus résistant au feu. Cependant, une augmentation encore plus importante du taux de conversion agricole n'a pas augmenté davantage la suppression des incendies, ce qui signifie que le paysage a atteint sa capacité maximale d'influencer le régime des incendies par des actions de lutte contre l'incendie. De plus, lorsque les terres agricoles étaient réparties en quelques grandes parcelles, l'efficacité était plus élevée (au même taux de conversion à des terres agricoles) et l'aire centrale des parcelles forestières était mieux preservé.

Dans le paysage agro-forestier fragmenté du sud-est du Canada, l'enrichissement des parcelles forestières fonctionnellement moins riches par des espèces d'arbres fonctionnellement différentes a eu un plus grand impact sur la diversité et connectivité fonctionnelle par rapport à ne cibler que les parcelles les moins ou les plus connectées. L'enrichissement multifonctionnel des parcelles fonctionnellement pauvres était encore plus efficace qu'une stratégie basée sur des plantations multi-spécifiques (faites au hasard ou dans des zones riveraines). De plus, enrichir avec des espèces résistantes aux ravageurs et parasites a réussi à réduire la mortalité induite par ceux-ci. Cependant, la plantation d'espèces tolérantes à la sécheresse n'a pas mieux réussi à prévenir la mortalité induite suite à une sécheresse que la stratégie visant à accroître la biodiversité globale du paysage.

Bien qu'il existe un nombre croissant de modèles pour simuler la dynamique du paysage et d'approches d'évaluation de la résilience des écosystèmes, les méthodes développées dans cette thèse visaient (1) à étudier les interactions spatialement explicites entre changements de couverture, comportement du feu et suppression des incendies; et (2) à évaluer les propriétés de systèmes complexes liées à la résilience des écosystèmes forestiers face aux perturbations naturelles et anthropiques de façon innovantes. D'abord, les changements d'utilisation du territoire peuvent-être modélisés comme un processus d'émergence-contagion, deuxièmement, le méta-modèle dynamique de paysage a un module d'extinction des incendies sensible à la configuration spatiale des combustibles, et troisièmement, les mesures de résilience des écosystèmes sont basées sur des traits fonctionnels de réponse des espèces et sur

la topologie du réseau spatial. De plus, dans les deux exemples, les approches de gestion du paysage suggérées sont totalement différentes de ce qui est en train d'être appliqué, ce qui remet en question les régimes de gestion conventionnels. En conclusion, cette thèse propose des méthodologies diversifiées et originales pour évaluer des scénarios de gestion forestière basés sur la résilience pour des paysages forestiers qui sont confrontés aux changements globaux.

Mots-clés: couplage de modèles; analyse de réseaux; régimes de perturbations; résilience de la forêt; aménagement du paysage.

ABSTRACT

Highly managed forest landscapes are complex socio-ecological systems exposed to multiple drivers of change. Their dynamics emerge from the multi-scale interplays between ecological processes, natural disturbance regimes, anthropic activities, and exogenous factors such as climate. Global changes are expected to interfere on these processes leading to decreases in the resilience of forest landscapes (i.e. the capacity to cope with and adapt to exogenous pressures and disturbances) to various single or compound disturbances. New forest management strategies adapted to these future environmental conditions need to be developed and investigated.

In this thesis, I present two simulation modelling approaches to characterise forest ecosystems to then evaluate landscape-scale forest management strategies to be applied in an uncertain global change context. All the proposed strategies seek at enhancing resilience of forest landscapes to shifting disturbances regimes. I apply each of these two modelling approaches to two distinct highly managed forest regions. Firstly, I explore the performance of large-scale fuel reduction policies in shaping the fire regime of a European Mediterranean fire-prone landscape using a landscape dynamic meta-model. I developed a spatially explicit land-use/land-cover change model which is then coupled to an existing spatially explicit fire-vegetation dynamics model. This meta-modelling framework was useful to study the variability on fire suppression effectiveness due to agricultural conversion. Agricultural land (a

low-load fuel that reduces fire intensity and allows fire brigades get closer to fire fronts) was allocated in the landscape at various annual rates, following a scattered versus an aggregate spatial pattern, and according to three storylines depicting potential fire management policies in the region. Secondly, I focused on understanding whether improving functional diversity or connectivity of a fragmented agro-forested landscape in south-eastern Canada fosters ecosystem resilience to natural and anthropogenic disturbances. Here, I introduced a multiscale evaluation of forest resilience based on the response of species functional traits and spatial network properties. I tested the approach to investigate if these alternative management strategies prevent decreases in resilience under future scenarios of drought, pest outbreak, and harvesting.

In the fire-prone Mediterranean landscape, I uncovered a non-linear relationship between the amount of new agricultural land allocated within the landscape and the fire suppression effectiveness. Fire suppression effectiveness barely increased at low / moderate annual conversion rates to agricultural land, but it sharply did at high annual conversion rates, meaning that land changes to a low-load fuel land-cover need to progressively accumulate before the system becomes more fire resistant. However, further increases on the agricultural conversion rate did not report clear benefits on fire suppression, meaning that the landscape reached its capacity of influencing the fire regime through fire-fighting actions. Moreover, when agricultural land was allocated in few large patches, effectiveness was higher (at the same rate of conversion to agricultural land) and forest core area was better maintained.

In the fragmented agro-forested landscape of south-eastern Canada, enrichment of the less functionally rich forest patches by functionally different tree species, rather than targeting either less or the more connected patches, had a larger impact in improving

both, diversity and functional connectivity at the landscape scale. Multi functional enrichment of functionally poor patches was even more cost-effective than a strategy based on multispecies plantations (at random or in riparian zones). Moreover, enriching with pest-resistant species was successful in reducing pest-induced mortality. However, planting drought-tolerant species did not do better at preventing drought-induced mortality than the strategy aimed at increasing overall biodiversity of the landscape.

Although there is an increasing number of models to simulate landscape dynamics and approaches to evaluate ecosystem resilience, the methods developed in this thesis to (1) investigate spatially explicit interactions between land-cover changes, fire behaviour, and fire suppression, and (2) evaluate system-level properties related to forest ecosystem resilience to natural and anthropogenic disturbances are innovative in several ways. First, land-use/land-cover changes are modelled as an emergence-contagion process, second the landscape dynamic meta-model has a fire suppression module sensitive to fuel loads spatial configuration, and third ecosystem resilience measures are based on species functional response traits and spatial network topology. In addition, in both examples, the landscape management approaches suggested are totally different from what is currently being done, challenging conventional management regimes. In conclusion, this thesis proposes broad and original methodologies to evaluate resilience-based scenarios for forest landscapes facing global changes.

Keywords: model coupling; network analysis; disturbances regimes; forest resilience; landscape management.

INTRODUCTION

Humans have always interacted with their surrounding environment, making their living out of natural resources and agriculture (Foley *et al.*, 2005). During the last three centuries, most rural societies progressively became industrialised, yet the human influence on the environment intensified and went way beyond the local scale (Goldewijk & Ramankutty, 2004; Ellis *et al.*, 2010). Nowadays, interactions between humans and the environment are not restricted to regional scales neither to short time spans, but are spatially globalised and have temporally broadened (DeFries *et al.*, 2004; Lepers *et al.*, 2005; Prins *et al.*, 2011). In coupled human-natural systems, entities of both sub-systems interplay to create unique complex systems with properties and dynamics not belonging to any of the sub-systems (Liu *et al.*, 2007). Human-natural systems, hierarchically self-organised around heterogeneous components, with non-linear dynamics emerging from multi (spatial, temporal, and hierarchal) scale interactions among them, with mechanisms that endlessly hold continual adaptive cycles of growth, accumulation, restructuring, and renewal (Levin, 1998; Gunderson & Holling, 2002). Indeed, feedback processes are typical of such complex systems, in which human activities alter the environment, while human well-being is affected by changes made on its environment (Liu *et al.*, 2007). Negative feedbacks decrease the effects on the response, stabilizing the system, while positive feedbacks amplify them and may force the system to change state. Like emergent properties, vulnerabilities and risks of these systems also come from the complex interactions between the components of both human and natural sub-systems (Turner *et al.*, 2003; Fischer *et al.*, 2016).

Forest landscapes as complex human-natural systems

Highly managed forest landscapes are adequate study models to assess the dynamics of complex human-natural systems (Parrott & Lange, 2013; Filotas *et al.*, 2014; Spies *et al.*, 2014). Landscapes are assemblages of natural and human-made features integrated in a considerable large area and result from cumulative spatio-temporal interactions between all entities herein. In forest landscapes, forest patches varying in size, composition, age, structure, and management condition are mostly intertwined with other vegetation (e.g. scrublands and prairies), agricultural lands, urban areas, water bodies, and road network (Cantwell & Forman, 1993). Many socio-economic activities (e.g. wood harvesting, crop irrigation, urban sprawl, tourism) have direct or indirect effects on forest ecosystems within these landscapes, altering forests composition, structure, and function (Foster *et al.*, 1998a; Thenail *et al.*, 2009). In addition, humans shape entire forest landscapes through land-use/land-cover change processes (i.e. transitions from one land-cover type to another) and active forest management (Dale *et al.*, 2000; Puettmann *et al.*, 2009). But in turn, changes exerted on these landscapes affect the capacity of forest ecosystems of providing essential ecosystem goods and services human well-being rely on (e.g. timber, carbon sequestration, water cycle regulation, pest control, crop production, and recreational activities) (Millennium Ecosystem Assessment, 2005; Carpenter *et al.*, 2006; Mitchell *et al.*, 2014).

One particularity of forest landscapes is that beyond anthropogenic pressures, natural disturbances such as wildfires, windthrows, insect outbreaks, landsides, or droughts are endogenous agents of system change (Attiwill, 1994). Natural disturbances are integral components of forest ecosystems, that are interlinked in many ways with both the human and the natural dimensions of the system (Raffa *et al.*, 2008; Pausas & Keeley, 2009; Moritz *et al.*, 2014). Disturbance regimes influence or trigger many ecological processes (e.g. regeneration, succession), drive spatial patterns of forest structure and composition, and create landscape heterogeneity through low and high intensity affected areas (White, 1979; Turner *et al.*, 2001). Spatial legacies and biological remnants (forest stands or trees not removed by the disturbance) likely determine the post-disturbance successional pathways of the vegetation (Franklin *et al.*, 2000). But the reverse is also true, patterns of vegetation structure and composition can to some degree dictate disturbances spreading and affectation. Hence, an insect pest will only target host trees and fires will likely spread according to fuel load spatial distribution (Turner & Romme, 1994; Holdenrieder *et al.*, 2004). But above all, humans have the capacity to directly or indirectly modify natural disturbances regimes through forest management, land-cover transitions, fuel reduction treatments, aerial spraying campaigns, and fire suppression among many actions (Keane *et al.*, 2002; Wermelinger, 2004; Syphard *et al.*, 2007; Pechony & Shindell, 2010).

Forest ecosystems, global change, and sustainable forest management

As complex human-natural systems, actual forested landscapes face global changes with a multitude of effects and challenges (Ayres & Lombardero, 2000; Rounsevell & Reay, 2009; Allen *et al.*, 2010; Reyer *et al.*, 2015). First, climate warming and extreme climatic events alter biological and ecological processes (e.g. phenology, seral succession, productivity), and most of the consequences are not fully understood yet (Cramer *et al.*, 2001; Johnstone *et al.*, 2010). Second, natural disturbances regimes are predicted to shift and move beyond their natural range of variability under changing climatic conditions, becoming more severe, large, and frequent (Turner, 2010; Sturrock *et al.*, 2011; Mori & Johnson, 2013). Even novel disturbances or compounded disturbances are expected to impact forest ecosystems in the near future (if this is not already the case), such as alien pest outbreaks, extreme episodes of drought, or wildfires favoured by extensive tree defoliation by insects (Brown & Johnstone, 2012; Buma & Wessman, 2012; Oliva *et al.*, 2014). Third, main historical land-cover changes have negatively impacted forest ecosystems though fragmentation and degradation by transforming natural lands to croplands or urban areas, and forest management has homogenised forest composition and structure by eliminating non-valuable timber species and promoting even-aged monocultures (Antrop, 2004; Puettmann *et al.*, 2009). But anthropic changes on forest landscapes are also supposed to shift (Alexander *et al.*, 2016). Yet, there is no clear consensus on future land-cover changes directions because these are system-dependent, obey to local to supra-national land management policies, and decisions are ultimately taken by single individuals, firms, or governments (Busch, 2006; van Asselen & Verburg, 2013). In general, land-use/land-cover changes have to satisfy increasing global demands for bio-energy, timber, food, water, and land for living (Balmford *et al.*, 2005; Banse *et al.*, 2011). These will potentially exert even more pressure on forest ecosystems. Lastly, what is even more relevant is that all these drivers of change are interlinked, influencing and even amplifying each other.

The isolated implications of climate change, shifting natural disturbances regimes, or land-cover changes on forest ecosystems are being closely analysed (Chakraborty *et al.*, 2000; Hanson & Weltzin, 2000; Cochrane & Barber, 2009; Prichard *et al.*, 2017). But the cascading effects of coupled perturbations on forest landscapes are largely unknown, being one of the big issues to address in a global change context (Paine *et al.*, 1998; Buma, 2015), that has started to capture the attention of landscape dynamic modellers (Schumacher & Bugmann, 2006; Seidl & Rammer, 2016). Therefore, the inherent uncertainty associated to future environmental and socio-economic conditions make prediction of forest ecosystem dynamics a major challenge, and sustainable forest management even a more daunting task (Kimmins *et al.*, 2007; Lawler *et al.*, 2010; Lindenmayer & Cunningham, 2013).

Nowadays, scientists, governments, managers, and stakeholders knowledgeable of forest ecosystems are more and more aware of intra- and inter-system connections, rapid environmental changing conditions, devastating effects of severe natural disturbances, climate warming, dependence on multiple forest ecosystem goods and services, out-dated methods and tools to represent forest dynamics, competition between land uses, and/or uncertain complex future for forest landscapes (Lawler *et al.*, 2010). Concurrently, we are slowly starting to be committed to sustainably managing forest ecosystems by building adaptive capacity of human-natural systems, to ensure forest function, and thus ecosystem services provisioning, now and in a long future (Folke *et al.*, 2002; Burton *et al.*, 2003; Bennett *et al.*, 2009; Allen *et al.*, 2011). On the whole, to achieve sustainability, forest landscape management should (1) target multiple objectives and quantify the unavoidable trade-offs, (2) recognise climate and natural disturbances regimes as permanents drivers of change, (3) incorporate the complexity of human-natural systems, and ultimately (4) foster forest landscapes and forest ecosystems resilience (Spittlehouse & Stewart, 2003; Cubbage *et al.*, 2007; Messier *et al.*, 2013; Rist & Moen, 2013).

Forest ecosystem resilience

Resilience is the capacity of a system to cope with exogenous constant pressures and high-intensity occasional disturbances, and learn from that process to be better adapted to future disrupting conditions (Holling, 1973, 1996; Gunderson, 2000). By coping with, it is understood that the system persists in its current form, keeping structure and function. Resilient systems have mechanisms to get unaltered or rapidly recover to the former state despite of cumulative degrading agents or sudden shifts in external conditions (Scheffer & van Nes, 2004; Cavers & Cottrell, 2015). Therefore, resilient forest ecosystems are those that through self-organization, adaptive strategies, and well-established regeneration patterns can maintain their main functions (Pausas *et al.*, 2004; Ennos, 2015). For example, boreal forests in eastern Canada are recurrently affected by spruce budworm (*Choristoneura fumiferana*), a defoliator insect whose main host trees are mature balsam firs (*Abies balsamea*) and black spruces (*Picea mariana*). Outbreaks tend to occur every 30-40 years (Boulanger & Arseneault, 2004). Insect communities and trees populations are perfectly synchronised and alternate cycles of depletion-renewal-growth-stabilization (Holling, 1973; Bouchard & Pothier, 2010). The wildfire season of 1988 devastated the Yellowstone Park and its surroundings. Scientist predicted an ecological catastrophe. A few years after, forest ecosystems rapidly and richly regenerated, whereas the whole landscape became even more heterogeneous than before the wildfires (Foster *et al.*, 1998b; Turner *et al.*, 1999; Kashian *et al.*, 2005). Similarly, in 2002 a large severe fire in an Australian plateau burnt three main forest formations: rainforest, wet sclerophyll forest, and dry sclerophyll forest. It was expected that the canopy cover of both rainforest and wet sclerophyll forest was irrevocably removed. Though, seven years later there was no evidence of floristic composition changes in any forest type (Knox & Clarke, 2012).

How to operationalise forest resilience

Even if there is empirical evidence that some forest ecosystems are resilient to natural disturbances, still little is known and agreed on how to guide forest landscape management to strengthen and enhance ecosystem resilience face to shifting disturbances regimes and climate change (Chapin III *et al.*, 2004; Olsson *et al.*, 2004). In fact, many international and national environmental initiatives and policies advocate for increasing resilience and adaptive capacity of forest (e.g. the guiding principles from the Environmental Protection Agency in USA (EPA, 2013), the Intergovernmental Panel on Climate Change (IPCC, 2014), or the Natural Resource Management Ministerial Council in Australia (NRMMC, 2009, 2010)). But at the operational level, a precise definition and appropriate ways to measure and monitor it are often not provided (Carpenter *et al.*, 2001; Sterk *et al.*, 2017). Indeed, managing for ecosystem resilience has used until now multiple interpretations and approaches (Chapin *et al.*, 2010). Millar *et al.*, (2007) for example, distinguished between strategies to improve either resistance, resilience, or even response capacity of forest ecosystems. Resistance options aimed at reducing forest exposure to disturbances, by for example, taking defensive actions in key strategic locations to avoid further incontrollable pest invasions. While strategies to improve response capacity to environmental change were based on assisted species migration, promoting species redundancy, and landscape connectivity (among others). As a measure of resilience some authors have proposed the time of recovery following a perturbation to return to the prior state (Newton & Cantarello, 2015), or even the rate of recovery defined at the species, stand, or ecosystem level, as the speed and extent these can restore to pre-disturbance levels (Palumbi *et al.*, 2008; Cole *et al.*, 2014). Other authors have focused on identifying potential recovery trajectories within the historical range of variability of the systems, as well as characterising the future range of variability to determine whether the system is resilience to changing disturbance regimes (Seidl *et* *al.*, 2016). All these multiple (and at the same time valid) approaches highlight a lack of consensus or general agreement on how to operationalise resilience and measure related concepts and properties (Rist & Moen, 2013; Timpane-Padgham *et al.*, 2017).

Conversely, to support decision-making processes targeting forest resilience in an uncertain global change context, the scientific community is already proposing updated innovative methodological approaches to uniformly evaluate and compare different forest landscape management regimes. For example, in the Great Lake forests (USA), the landscape dynamic model LANDIS-II was used to simulate four management strategies under three scenarios of climate change (a business-as-usual intensive even-aged management, an increase of protected areas in riparian zones, a less intensive management regime with longer rotation periods, and an assisted migration strategy of southern species as a mean to increase adaptability to a warming climate) and test the outcomes in terms of functional diversity following a wildfire (Duveneck *et al.*, 2014; Duveneck & Scheller, 2016). The forest growth Forest Vegetation Simulator model was used to simulate the carbon dynamics of three planting treatments after disturbance (no action, a resilience-oriented strategy by planting local species, and a adaptation-oriented strategy by planting climatically suitable species) in southern Rocky Mountains (USA) (Buma & Wessman, 2013). Coupling a stand-level, forest-level, and habitat model served as a framework to support the decision-making process in development and implementation of a sustainable forest management plan for a region in north-eastern British Columbia (Canada) (Seely *et al.*, 2004).

In this thesis, I aim at contributing firstly, to the body of knowledge and work on quantitative robust methods and tools to address resilience-target forest landscape management questions in a context of global change and uncertainty (de Senna

Carneiro *et al.*, 2013). Such analytical frameworks should (1) account for the complexity of forest landscapes understood as coupled human-natural systems, (2) include all the key elements, processes, and interactions driving system dynamics at the right spatial and temporal scales, that is incorporate the main anthropogenic (land-use/land-cover changes and forest management), natural (fires, insect outbreaks, windthrows), and climatic factors of change, (3) allow exploring different scenario storylines, that is, alternative landscape management strategies never applied before, (4) be designed to support landscape-scale decision-making processes and favour participative scenario building, (5) incorporate uncertainty, and as much as possible, and (6) be spatially explicit (Kelly *et al.*, 2013; Verburg *et al.*, 2013; Rammer & Seidl, 2015).

Secondly, I aim at proposing a generic multi-evaluation of forest ecosystems resilience to disturbances. Other than characterise system resilience, it allows to measure the response of resilience-target managed forest landscapes too. This quantitative approach is based on species functional response traits to measure functional redundancy and response diversity, and network properties of the forest landscape viewed as a network of forest patches (Elmqvist *et al.*, 2003; Pillar *et al.*, 2013; Craven *et al.*, 2016). A network is a theoretical model of interconnected heterogeneous elements, represented as nodes connected by links. Networks have proved to be excellent models to capture the complexity of many systems, and network theories and analysis useful tools to describe structure, function, emerging properties, and system behaviour to node-removing, link-removing, and spreading-like disturbances (Newman, 2003; Boccaletti *et al.*, 2006). Finding out properties and behaviours of forest networks studied for network archetypes, allows to extrapolate resilience-system features from theory to practice (Shirley & Rushton, 2005; Barthélemy, 2011).

Thesis objectives and structure

The main objective of this thesis is to advance in building methodological approaches that (1) capture the complex dynamics of anthropised forest landscapes and/or (2) allow to quantitatively evaluate alternative landscape-scale forest management scenarios. Most of my current research questions focus on how forest ecosystems have to be managed today to become more resistant / resilience to current and future natural disturbances regimes (Carpenter, 2002). To this end, management strategies proposed here are to be applied in an uncertain global change context to face potential natural and anthropogenic perturbations impacting forest landscapes. I have selected two highly humanised forest landscapes to illustrate the application of these methodologies. The first landscape is Catalonia, a European Mediterranean region in northeast Spain. Catalonia is recurrently impacted by large intense wildfires during the summer season, forest mosaics have been homogenised in the last four/five decades due to rural depopulation, and enjoys a cutting-edge group of wildfire fighting specialists that focus on understanding interacting factors driving wildfires as an inherent part of Mediterranean ecosystems (among others) (Valladares *et al.*, 2014; Otero & Nielsen, 2017). The second landscape is Centre-du-Québec region, an agro-forested mosaic lying on the eastern edge of the Saint Lawrence river in south-eastern Canada (Craven *et al.*, 2016). Forests of Centre-du-Québec have been fragmented and homogenised by agricultural and timber harvesting activities, pest outbreaks and severe droughts are imminent threats, and most silvicultural management is still single-focus (Holling & Meffe, 1996; Dymond *et al.*, 2010; Dodds & Orwig, 2011; Allen *et al.*, 2015).

The thesis objectives are addressed in three distinct but related chapters, even if each of them has been written as stand-alone.

Chapter 1 presents a generic spatially explicit land-use/land-cover change model to simulate any land transition following a demand-allocation approach. In a demand-allocation land-use/land-cover model, for every land transition, the demand is the quantity of land that have to change to the target land-cover (e.g. urban infrastructures for urbanization), while the model itself is responsible of the allocation of that demand, that is the spatialization of the change. In my modelling framework, the spatial allocation procedure builds on the assumption that land transitions occur in two phases: change occurrence and change spreading (or contagion) (Rosa *et al.* 2013). The procedure works with three parameters: rate of change occurrence, rate of change spreading, and acceleration of change-contagion. With a sensitivity analysis, I showed how the relation between change occurrence and change spreading determine the emergence and extent of multiple patterns of patches-of-change. I integrated this allocation procedure to the spatial explicit land-use/land-cover change model MEDLUC that mimics urbanisation, rural abandonment and agriculture conversion in Catalonia (at two spatial resolutions 1 km^2 and 1 ha).

Chapter 2 explores the spatial interactions between vegetation dynamics, wildfires, land-cover changes, and fire suppression by adopting a landscape dynamic meta-modelling approach. I built a meta-model by coupling the land-use/land-cover change model MEDLUC developed in Chapter 1 to the spatially explicit fire-succession model MEDFIRE already calibrated for Catalonia (Brotons *et al.*, 2013). This new tool accounts for multiple interacting natural and anthropic factors of change driving dynamics of highly anthropised Mediterranean forest landscapes. I used it to explore plausible fuel load reduction management regimes based on agricultural conversion of scrublands and marginal forests (Moreira & Pe'er, 2018). Landscape management strategies sought at create more heterogeneous mosaics that could increase fire suppression effectiveness to ultimately shape the fire regime. I tested two contrasting hypotheses about non-linear responses of fire reduction over the landscape heterogeneity gradient. Supported by percolation principles (Turner *et al.*, 2001), new agricultural patches can enhance fire extinction capacity because high burnable fuels will progressively become less connected, being the fire spread behaviour non-linear close to the theoretical percolation threshold.

Chapter 3 presents an innovative multi-criteria evaluation of forest ecosystems resilience to natural and anthropogenic disturbances based on species functional response traits and spatial network properties. The approach considers response diversity, functional redundancy, network connectivity, modularity, and centrality as key components /indicators of forest resilience. I first applied it to characterise the Centre-du-Québec region using a network representation of forest patches. Then, I investigated the variation of these five properties under distinct resilience-based management scenarios and following three main disturbances: drought episode, pest outbreak, and timber harvesting. The set of designed scenarios evaluated how resilience related properties behave according to (1) the amount of area managed, (2) the management strategy applied - functional enrichment of current forest patches versus plantation of new patches -, and (3) the species-trait function prioritised in the sylvicultural intervention. I tested the hypotheses that natural disturbances (drought and pests) exert a stronger effect on ecosystem response diversity and functional redundancy than harvesting, that functional connectivity was largely decreases by harvesting (rather than by natural disturbances), but that all management strategies could prevent to some extent ecosystem resilience loss.

Finally, the main contributions, findings, and concluding remarks of my work are summarised in the last section of this thesis.

CHAPTER I

A SPATIAL ALLOCATION PROCEDURE TO MODEL LAND-USE/LAND-COVER CHANGES: ACCOUNTING FOR OCCURRENCE AND SPREAD PROCESSES

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1.1 Abstract

Land-use/land-cover (LULC) change models integrate the effects of anthropogenic drivers of landscape change. Spatially explicit LULC change models help at understanding the landscape mosaic that emerges from the interplay between local-scale decisions as well as regional and national policies. These models produce valuable spatially explicit scenarios of LULC change that underpin biodiversity impact and ecosystem services assessments. Most raster-based LULC change models adopt the demand-allocation approach to simulate land transitions (i.e. the transformation of one land-cover type to another for a given spatial unit). In a demand-allocation framework the expert fixes the demand (or quantity of change) and the LULC change model uses a spatial procedure to allocate the change (i.e. to select the cells to be transformed to the target land-cover type). Here, we propose a spatial allocation procedure that builds on the assumption that land transitions occur in two phases: change occurrence and change spreading (or contagion). The allocation procedure uses a sorted queue of cells waiting to undergone change. Three parameters (rate of change occurrence, rate of change spreading and acceleration of change-contagion) control the order of cells order in the queue, and ultimately determine the emergence and extent of patches-of-change. We performed a sensitivity analysis where we show that the relation between both rates (i.e. change occurrence and change spreading) allows patches-of-change expand before other patches arise or vice versa. We provide a simple protocol to implement the allocation procedure as the core of a spatial explicit LULC change model, and we applied this protocol in the development of a new model, called MEDLUC, that intends to replicate the most relevant transitions observed in Mediterranean landscapes: urbanisation, rural abandonment and agriculture conversion. For Catalonia, a region in NE Spain, MEDLUC reproduces the empirical patches-of-change distributions from a 16-year period at two spatial resolutions (1 km^2 and 1 ha). Overall, our allocation procedure performs better than a null model for urbanisation and rural abandonment at both resolutions, while it does worse when modelling agriculture conversion.

Keywords: Land Transitions; Transition-potential; Demand-allocation approach; Change occurrence; Change spreading; Power-law

1.2 Introduction

Land-use/land-cover (LULC) spatial distribution emerges from the dynamic interplay between human and natural complex systems. Models of LULC change have become helpful tools to test hypotheses about anthropogenic and environmental drivers of change, to investigate feedback dynamics, as well as to anticipate possible future landscape changes (Brown *et al.*, 2013). Two broad classes of LULC change models have independently emerged within social and natural sciences (Geoghegan *et al.*, 1998). Based on household surveys, agent-based models developed mostly within social sciences simulate the decision-making processes that result from the interactions among individuals and the environment (Parker *et al.*, 2003). In many applications, agent-based models are used to explore land systems from a theoretical perspective (Janssen & Ostrom, 2006; Matthews *et al.*, 2007) and are restricted to relatively small areas (Valbuena *et al.*, 2010). Because agent-based models seldom incorporate explicitly the spatial dimension of the system, they have been mainly used to understand the processes rather than to project scenario outcomes, but see Gibon *et al.*, (2010). On the other hand, based on remote sensing imagery, interpreted orthophotos, or historic cartography, LULC studies in natural sciences first focused on recognizing land-cover spatial patterns and then on spatially characterizing land transitions and the processes underlying them. This knowledge was later used to develop spatially explicit LULC change models based on the empirical relations between observed drivers of LULC and resulting various landscape configurations (Veldkamp & Lambin, 2001). These modelling frameworks can integrate climatic, biophysical, or socio-economic factors of change operating from local to global scales to relate causes and consequences of LULC changes (Lambin *et al.*, 2001).

Spatially explicit LULC change models applied in a variety of research contexts have been used to anticipate and predict the effects of multiple land transitions on regional climate, greenhouse gas emissions, biodiversity, and socio-economic welfare at a range of different spatio-temporal scales (Rounsevell *et al.*, 2006a; Schulp *et al.*, 2008; Nelson *et al.*, 2009). Since LULC maps are essential for local and regional assessments of ecosystem service provisioning, the importance of LULC modelling has strongly increased in recent years (Metzger *et al.*, 2006). In the future, models of this kind may become fundamental tools to accurately inform policy makers and land managers committed to sustainable development, biodiversity conservation, and/or climate warming mitigation (Rounsevell & Reay, 2009; Renwick *et al.*, 2013). To be used for this purpose, LULC modelling tools need to be able to translate socio-economic trends or future land policies into spatially explicit LULC change projections that are easily interpretable and suitable to integrate in multidisciplinary assessments (Turner *et al.*, 2007). However, this is not always the case, especially if the assumptions underlying land transitions are not made explicit or if the algorithms employed to spatialize scenario storylines are too complex and/or ambiguous. Thus, what often determines reliance on a spatially explicit LULC change model in a decision-making context is the model's transparency and flexibility, as well as the availability of standard procedures to validate the model and quantify the uncertainty on results (Sohl & Claggett, 2013).

To model the complex social and ecological dynamics of any coupled human-environment system, many spatially explicit LULC change models have adopted the demand-allocation principle. In a demand-allocation framework, the quantity of change (i.e. the demand) is independently estimated first, followed by the spatialization of these quantities (i.e. the allocation) (Verburg *et al.*, 2002). The two main advantages of this modular structure are: (1) model validation can be split in two independent analyses to better isolate different sources of error and uncertainty

(Pontius *et al.*, 2004; Camacho Olmedo *et al.*, 2015), and (2) since drivers of the quantity of change may not be the same as those driving the spatial location of change, this structure allows estimating both according to the most appropriate socio-economic and environmental factors (Veldkamp & Lambin, 2001). To apply this modelling approach to study the behaviour of a socio-ecological system, a previous step is to identify and describe the set of land transitions that potentially will take place on the system. A land transition is the transformation of a land-use/land-cover type (hereafter LCT), or a set of them, to a target LCT. For example, urbanisation may be defined as the transition between bare soil and abandoned crops to housing covers, while rural abandonment may be defined as the transition between agricultural lands to semi-natural vegetation areas. In many applications, the demands are externally assessed using specialized quantitative socio-economic models (Asselen and Verburg 2013). Therefore, the key differences between demand-allocation LULC change models arise from the approach used to dynamically allocate the quantity of change in space.

Most common spatially explicit LULC change models rely on regression-type methodologies to integrate socio-economic and biophysical factors of change. They derive either potential-transition maps that indicate the likelihood of a land transition (Pérez-Vega *et al.*, 2012) or potential-occurrence maps that indicate the spatial suitability of land-cover types (Verburg *et al.*, 2002; Castella & Verburg, 2007). Both types of maps are used to stochastically forecast the location of changes (i.e. the maps become the probabilistic basis to spatially-allocate the demand) (Poelmans & Van Rompaey, 2010). For example, the large family of CLUE models bases the spatial allocation on empirical multivariate logistic regressions (Verburg *et al.*, 2002; Castella & Verburg, 2007; Verburg & Overmars, 2009). Spatial land-cover type suitability, derived from biophysical and socio-economic drivers specific of the studied region, leads the iterative spatialization of the demand while considering competition between land-cover types for the most productive locations. Artificial neutral networks allow the integration of empirical data to learn about past functional relationships and, for example, predict urbanisation (Pijanowski *et al.*, 2002) or deforestation (Mas *et al.*, 2004). Some disadvantages of regression-type data-based methodologies are: (1) they do not allow distinguishing between empirically-good predictors of changes from the spatio-temporal mechanisms that determine occurrence, extent, and spatial configuration of changes (Rosa *et al.*, 2013); (2) they are constrained by data availability of all the drivers of change at the spatial resolution of the model (Sohl *et al.*, 2007); (3) the relations are static (Poelmans & Van Rompaey, 2010); and (4) they do not focus on the explicit modelling and validation of the spatial patterns of land-cover change (Brown *et al.*, 2002).

It has been argued that LULC change processes (chiefly urban development) are self-organising, path-dependent phenomena (Wu, 2002). On one hand, this means that although macroscopic patterns are regulated by upper-level administrative policies, they emerge from local factors, individual behaviours and the corresponding interactions (Verburg *et al.*, 2004). On the other hand, this also implies that land changes derive from two interrelated processes: occurrence (or origination) and spreading (Clarke *et al.*, 1997; Soares-Filho *et al.*, 2002). A large family of models aiming to capturing these two processes have relied on a cellular automata (CA) approaches (White & Engelen, 2000). A CA operates over a *n*-dimensional grid, each cell is in a discrete system state (i.e. a LCT), and it updates to a new state according to the composition of the neighbourhood and specific expert-defined transition rules. Mainly applied to simulate urban growth, CA have also been useful to spatialize the dynamics in Amazonian landscapes (Soares-Filho *et al.*, 2002). Customized cellular automata may allow for a higher control of when patches-of-changes initiate and how (or where) they expand (Ward *et al.*, 2000; Liu & Phinn, 2003). But CA-based models operating at regional scales have been revealed to be extremely difficult to calibrate for reproducing multiple, real LULC changes (Straatman *et al.*, 2004; Dietzel & Clarke, 2007). Therefore, there is a need of approaches capable of modelling multiple LULC changes accounting for both occurrence and spreading in a simple yet flexible way.

Here, we introduce a new spatial demand-allocation procedure for modelling LULC change dynamics. The novelty of this procedure is that it explicitly addresses the two phases inherent on land transitions: (1) land change occurrence (i.e. origination of a new patch-of-change) and (2) change spreading (or the spatial contagion of the land transition) that will generate the final spatial extent and configuration of that patch-of-change. LULC change occurrence and spreading have been identified as critical phases to explain observed patterns of land change, for example, those generated by deforestation in the Amazon (Rosa *et al.*, 2013), or by urbanisation in Europe (Antrop, 2004). Our objective is two-fold: (a) To show that discretising land-cover transitions in two phases, occurrence and spreading, while assigning to these two processes variable rates can generate emergent patches-of-change that reproduce realistic spatial patterns of land-cover change; and (b) to show that the proposed allocation procedure is capable of reproducing multiple observed transitions at multiple spatial scales. We chose a regional landscape in the Mediterranean basin to test the applicability of our procedure and its ability to replicate empirical spatial patterns of change derived from urbanisation, rural abandonment, and agriculture expansion processes at 1 km^2 and 1 ha.

In the following section we first present in detail the proposed spatial demand-allocation procedure and provide basic guidelines to integrate it within a generic spatially explicit LULC modelling framework. We then address (a) by means of a sensitivity analysis using neutral landscapes. After that, we describe how we built

MEDLUC, a spatially explicit LULC change model that simulates urbanisation, rural abandonment, and agriculture expansion transitions in Catalonia (NE Spain). Finally, we address (b) by presenting a validation exercise of the MEDLUC model (at two spatial resolutions) based on the assumption that patches-of-change size distributions follow a power law distribution.

1.3 Methods

1.3.1 The spatial demand-allocation procedure

We designed the spatial demand-allocation procedure to capture variability in the degree of spatial aggregation of transitions between land-use/land-cover types. Here LCT transition refers to specific state-changes between LCTs. Our procedure focuses on the distinction between two phases of land transitions: the occurrence and the spreading of changes. We assume that the following elements are available: an initial LULC raster map (with a certain number of LCTs), the definitions of the LCT transitions of the system, and the allocation demand D_{lct} for each transition. D_{lct} is the number of cells that will change to the targeted LCT in a way that the quantity of change for that transition will be satisfied. For each LCT transition, a spatial *transition-potential* variable describes the transition potential to the targeted LCT. This spatial variable accounts for the biophysical, cultural, and socio-economic drivers behind that transition, as well as the land use history or neighbourhood characteristics (Dendoncker *et al.*, 2007). If *transition-potential* is not a probability of change (with its corresponding density function, derived for example from a logistic model) then it is used as a weighting variable. That is, its range of values is linearly scaled to [0, 1] and then it is used to prioritize the locations to undergone change. If the *transition-potential* variable is not specified, then all cells are assumed to have equal potential.

The algorithm to allocate the demand D_{lct} of a LCT transition for a given time step works as follows (Figure 1.1): D_{lct} cells are randomly selected according to the *transition-potential* variable. The selected cells (hereafter called *initiating cells*) form the pool of cells from which patches-of-change may originate. An initiation time value (T_{ini}) drawn from an exponential distribution with rate λ_i is assigned to each *initiating cell* (see Equation 1). *Initiating cells* are sorted in a queue by ascending order of their T_{ini} values. The first cell of the queue (i.e. the cell with minimum T_{ini}) is then processed in six steps:

1. The location on the LULC raster map updates to the targeted LCT.
2. The cell is removed from the queue of active cells.
3. The demand is decreased by one unit.

If the demand still to be allocated is greater than 0:

4. Its cardinal (rook) neighbours that can potentially change and have not already changed are activated; hereafter called *spreading cells*. Only neighbour cells that can switch to the targeted LCT can become *spreading cells*.
5. For each *spreading cell* recently activated a value is drawn from an exponential distribution with rate λ_s. It is scaled by $(T_{ini})^k$, where T_{ini} is the processing time of the *initiating cell* of that patch-of-change, and added to T_{src}, the time of the cell that caused the activation (either an *initiating cell* or another *spreading cell*). The result of this operation is the spreading time of that cell (T_{sprd}) (see Equation 2).

6. *Spreading cells* are added to the above-mentioned queue of cells according their spreading time values.

The next first cell on the queue (i.e. the cell with smallest time, T_{ini} or T_{sprd}) is processed following the same six steps, until all the demand is allocated. If the next cell at the front of the queue is from the *initiating cells* pool, a new patch-of-change will originate. However, because the T_{sprd} of a *spreading cell* can be lower than any T_{ini} of the *initiating cells* currently on the queue, the *spreading cell* can become the next cell to be processed. In this case an existing patch-of-change will expand instead of originating a new patch. This is the mechanism that allows a LCT transition to spread through neighbouring cells. Once the demand is fully allocated, any cell remaining on the queue is discarded. The two equations that determine processing times for activated cells are:

$$T_{ini} \sim \mathrm{NEGEXP}(\lambda_i) \quad [1]$$

$$T_{sprd} \sim \mathrm{NEGEXP}(\lambda_s) \cdot (T_{ini})^k + T_{src} \quad [2]$$

Parameters λ_i, λ_s and k are quantities that stochastically control the speed of patch occurrence and spreading processes, to ultimately determine the spatial pattern of a transition. The *transition-potential* spatial variable is only used in the selection of the *initiating cells* pool, but the activation of the *spreading cells* is controlled by the $\{\lambda_i, \lambda_s, k\}$ parameter set. The speed of occurrence of new patches is regulated by parameter λ_i (or rate of change-occurrence). Setting λ_i to larger values will lead to smaller times for patch creation (patches-of-change will be created relatively quickly) and hence the demand will more likely be allocated in a large number of relatively small patches. Parameter λ_s (or rate of change-contagion) is related to the rate at which the *spreading cells* are induced to change. Spatial patterns of LULC change will emerge from the interplay between λ_s and λ_i, i.e. how fast patches expand in relation to formation of new patches. At higher values of λ_s the value of the exponential distribution will likely be small, and T_{sprd} will be closer to T_{src}. In such cases, if the rate of patches-of-change occurrence is low, cells undergoing change may aggregate around the initial cell, creating patches of larger size. Finally, parameter k controls the acceleration at which *spreading cells* are induced to change, i.e. it is the acceleration of change-contagion. In the algorithm, the parameter k controls the relative position of the *spreading cells* in the ascending-ordered queue in relation to the initial source cell. In other words, k regulates the inheritance between patch-of-change formation rate and change expansion. While λ_s influences the growth rate of patches-of-change equally (i.e. all faster or slower once initiated), k influences the growth rate of patches-of-change relative to the initiating time of the cells that originated them.

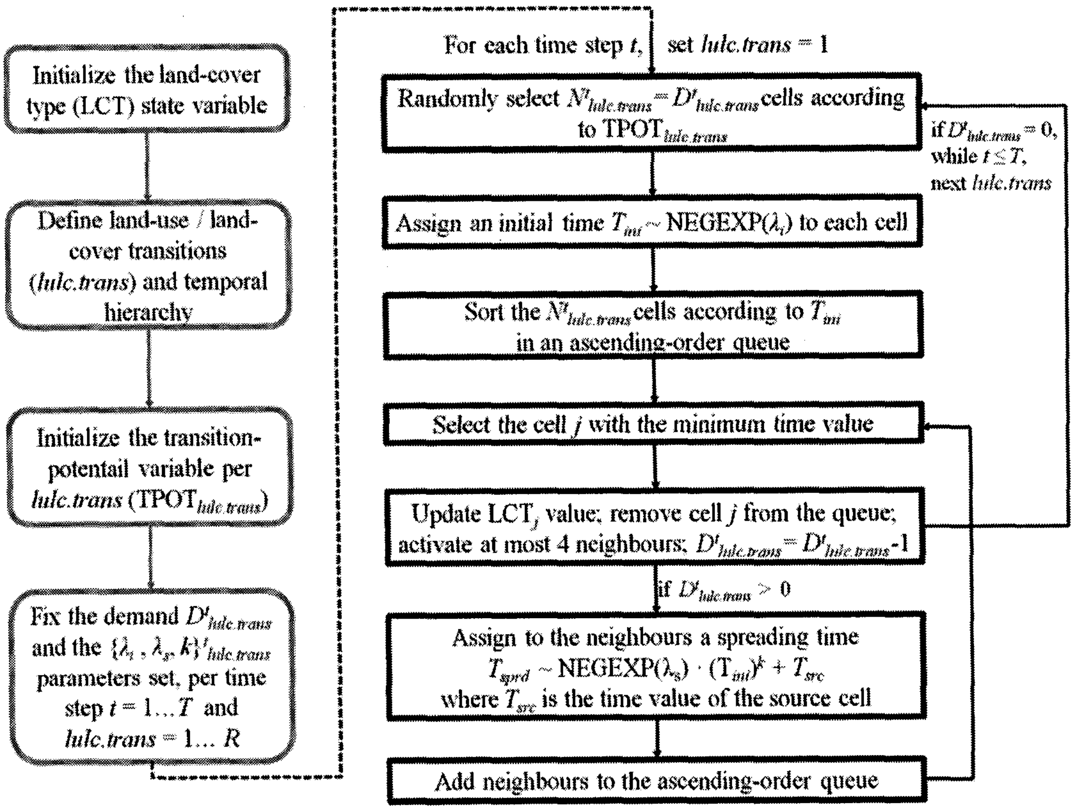

Figure 1.1: Flow diagram of the spatial procedure that uses an ascending-order queue of pixels susceptible to undergone change to allocate the demand of a land-cover transition (black squared boxes). The demand-allocation procedure is embedded in MEDLUC model's working diagram (grey boxes are all user-defined).

The spatial demand-allocation procedure can be used as the core of a spatially explicit LULC change model to simulate the LCT transitions of a given socio-ecological system. For clarity, here we summarize the required actions a modeller should perform beforehand (Figure 1.1):

a. Initialise the spatial state variable accounting for the main LCTs of the system as a raster layer.

b. Define the LCT transitions of the system by identifying the LCTs that are allowed from each target LCT. If there is more than one transition allowed for a given target LCT, then a sequence of transitions or temporal hierarchy has to be detailed (Rounsevell *et al.*, 2006b).

c. Set the minimum sojourn time per land-transition, sensu Soares-Filho *et al.*, (2002). That is, the time span required to allow cells be affected by another land-transition after having changed.

d. For each LCT transition, initialise the *transition-potential* variable. If it depends, among other factors, on the LCT spatial structure, the *transition-potential* will be dynamically updated.

e. Fix the time horizon and the time step at which transitions occur.

f. Estimate the demand for each transition at each time step. Demand units can be specified as number of cells or percentage of new cells (over the area occupied by the targeted LCT or the whole area).

g. Determine the $\{\lambda_i, \lambda_s, k\}$ parameter set for each transition. The parameter set can be dynamic, varying at each time step if needed.

The output of the model (per time step) are the LCT state variable updated, an auxiliary variable indicating the updated locations per land-transition, and a secondary state variable accounting for the time since the last change.

1.3.2 Sensitivity analysis of the demand-allocation procedure

We performed a sensitivity analysis to estimate the influence of each parameter from the demand-allocation procedure (λ_i, λ_s, and k) on the final spatial distribution of the patches-of-change. To conduct the sensitivity analysis, we implemented a spatially explicit LULC change model based on neutral landscapes (Li *et al.*, 2004; Gardner & Urban, 2007). We used the SIMMAP software (Saura & Martínez-Millán, 2000) to generate a squared landscape of 180 km per side (32 400 km^2) at 1 km^2 of resolution, with four LCTs (urban, vegetation, agriculture, and water), and the level of fragmentation p set at 0.50. The parameter p specifies the spatial aggregation of the LCT, and ranges from 0 -total randomness- up to 1 -perfect aggregation-. Our reference to determine the LCTs and their abundance on the landscape was the European Environment Agency tree classification system adopted for the CORINE Land Cover (CLC) Program. The relative abundances of LCTs were fixed at 2 % urban, 47 % vegetation, 50 % agricultural land, and 1 % water. They correspond to the 1990 CLC abundances for the Mediterranean biogeographical region (EEA, 2006). The sensitivity analysis was conducted for rural abandonment only (i.e. conversion of agricultural land to natural / semi-natural vegetation). The demand was proportional to the amount of change observed in the Mediterranean region between 1990 and 2006 CLC datasets (EEA, 2006). We fixed a single time step at 16 years (covering the entire time period). Because neutral landscapes were void of biophysical or socio-economic drivers of change, the *transition-potential* spatial variable was set equal for all cells, meaning that there was no spatial priority where patches arose. We designed a combinatorial set of experiments in which each parameter took a value from the following subsets: {0.05, 0.1, 0.25, 0.5, 1, 2.5, 5, 10, 15, 20} for λ_i and λ_s; {0.1, 0.3, 0.5, 0.7, 0.9} for *k*. For each experiment we replicated the demand-allocation procedure 20 times.

We verified that most of the patches-of-change size distributions could be approximated using a power law statistical distribution. This means that, for the discrete variable patches-of-change size abundances *S*, if $\{p(s)\}$ denotes the set of discrete probabilities,

$$p(s) \propto s^{-\beta} \qquad [3]$$

The β exponent of a power-law distribution identifies which are the predominant sizes. As β increases (and β is over 1) small patches-of-change account for an increasingly larger proportion, when β <1 larger patches tend to dominate, and when β =1 all patch sizes have equal contribution to the overall distribution.

Power law distributions present heavy long upper tails because most of the samples gather around low values. Instead of characterizing this type of distribution by a common histogram, Pueyo (2006) suggested to use a histogram with multiplicative intervals for the bins. When the discrete probabilities $\{p(s)\}$ are standardized by the size of the bin, we obtain the density of probability per bin $\{f(s)\}$ than can be further compared. Following Pueyo (2006), we took multiplicative intervals $[L^j, L^{j+1}]$ with $L = 2$, and computed the central value $s_j = 2^{j+1/2}$ and the estimated probability density $\hat{f}(s_j) = \frac{1}{2^j} \cdot \frac{n_j}{N}$ of bin *j*, where n_j is the number of patches in bin *j* and *N* the total number of patches. As the series $\{s_j, \hat{f}(s_j)\}_j$ verifies Equation 3, we took logarithms to fit the parameter β by linear regression. Using this approach we obtained an estimation of β for each experiment and replicate.

We characterized the spatial patterns of patches-of-change using four class metrics (Gustafson, 1998; Li *et al.*, 2004): (i) the number of patches relative to the total demand allocated (i.e. the number of patches needed to allocate a 100-cell demand), (ii) the mean patch size, (iii) the maximum patch size, and (iv) the maximum fractal dimension index that describes the shape complexity of the patch (i.e. the irregularity on its perimeter), and is estimated as two times the logarithm of the patch perimeter divided by the logarithm of the patch area. We fitted log-log linear regressions between each response variable (the β exponent and the four class metrics) and the λ_i, λ_s, and k parameters plus their respective interactions ($k \times \lambda_i$, $k \times \lambda_s$, $\lambda_i \times \lambda_s$), acting as independent variables. Responses to these factors were evaluated using analysis of variance. Analyses were conducted in the R statistical environment (R Development Core Team, 2008), using the functions provided in the 'poweRlaw' (Gillespie, 2014) and 'SDMTools' (VanDerWal *et al.*, 2014) packages.

1.3.3 Modelling LULC changes in a Mediterranean region using a spatially explicit demand-allocation LULC change model

European landscapes have historically evolved under a myriad of environmental and anthropogenic forces, leading to heterogeneous urban-rural matrices (Antrop, 2004). In the last decades many regions have experienced severe land transformations due to both exogenous (market liberalization, immigration, climate change) and endogenous (economic growth, population aging) driving factors. In Mediterranean countries the processes of land abandonment, agriculture expansion, and urbanisation (e.g. city expansions, urban sprawl, and second home proliferation) interacting with wildfires have largely shaped landscapes and altered ecosystem functioning during the last years (Moreira *et al.*, 2011; Stellmes *et al.*, 2013). We chose the northwest region of Catalonia, Spain (Figure 1.2) as representative of the three main LULC changes taking place in Mediterranean landscapes. In Catalonia, fire incidence (ca. 10 % of the territory burnt since the 80's decade) and LULC change processes mostly explain the observed recent transformations on landscape composition and configuration (Díaz-Delgado & Pons, 2001; Badia *et al.*, 2011; Puerta-Piñero *et al.*, 2012) (Table 1.1).

We designed a LULC change model called MEDLUC (MEDiterranean LUlc Change) to spatially simulate the land transitions most frequently occurring in European-Mediterranean landscapes: urbanisation, rural abandonment, and agriculture expansion (Verburg *et al.*, 2010). MEDLUC was implemented in the SELES landscape modelling platform (Fall & Fall, 2001) and is available under request. Following the protocol of the previous section (Figure 1.1), MEDLUC specifications for Catalonia are:

a. We initialize the land-cover types spatial state variable using the 1993 Land Cover Map of Catalonia (www.creaf.uab.es/mcsc). Its hierarchic legend was re-classified into four major categories (Figure 1.2): urban areas and human-made infrastructures (e.g. roads), natural and semi-natural areas (e.g. forests, scrublands), agricultural land (e.g. crops, vineyards, orchards), and others (comprising water bodies and bare soil). The series of Land Cover Maps of Catalonia are categorical vector maps derived by photo interpretation of orthophotos. We rasterised the 1993 version at 1 km^2 and 1 ha spatial resolutions.

b. We defined three land-cover transitions: *urbanisation* being the transition from natural vegetation and agricultural lands to urban areas, *rural abandonment* being the conversion from agricultural land to and semi-natural areas, and *agriculture expansion* being the inverse of rural abandonment. Urbanisation is modelled first, followed by agriculture expansion and, lastly, rural abandonment. This temporal hierarchy of the land-cover transitions is consistent with the amount of human effort or investment required.

c. We did not have to fix the minimum sojourn time for any transition because only one time-step was simulated (see below).

d. We wilfully decided to not deeply explore the actual biophysical and socio-economic drivers of each land transformation. However, vicinity composition of the cells subject to change and spatial interactions are relevant factors of change (White & Engelen, 2000; Dendoncker *et al.*, 2007). Thus, we adopted the neighbour factor approach introduced by Verburg *et al.* (2004) to initialize the *transition-potential* variable. The neighbour factor $F_{i,l,d}$ characterizes the weighted influence of the LCT l within the neighbourhood d of cell i. We considered a square neighbourhood d of 3 km size to compute it.

e. The time horizon was fixed in 2009 and the demand was allocated in a single time step of 16 years.

f. We reclassified the 2009 version of the Land Cover Maps of Catalonia series to the four major land-cover categories mentioned above. We assessed by cell-to-cell differences the demands of urbanisation, rural abandonment, and agricultural expansion at both spatial resolutions (Table 1.1).

g. The $\{\lambda_i, \lambda_s, k\}$ parameter set for each LCT transition and spatial resolution was set by calibration (see below).

Table 1.1: Observed land-cover change demands in Catalonia from 1993 to 2009 for the three land transitions, at 1 km^2 and 1 ha of spatial resolution derived from the Land Cover Maps of Catalonia.

Demand for : at :	1 km^2	1 ha
Urbanization	579	68 999
Rural abandonment	1 319	159 915
Agriculture expansion	112	35 494

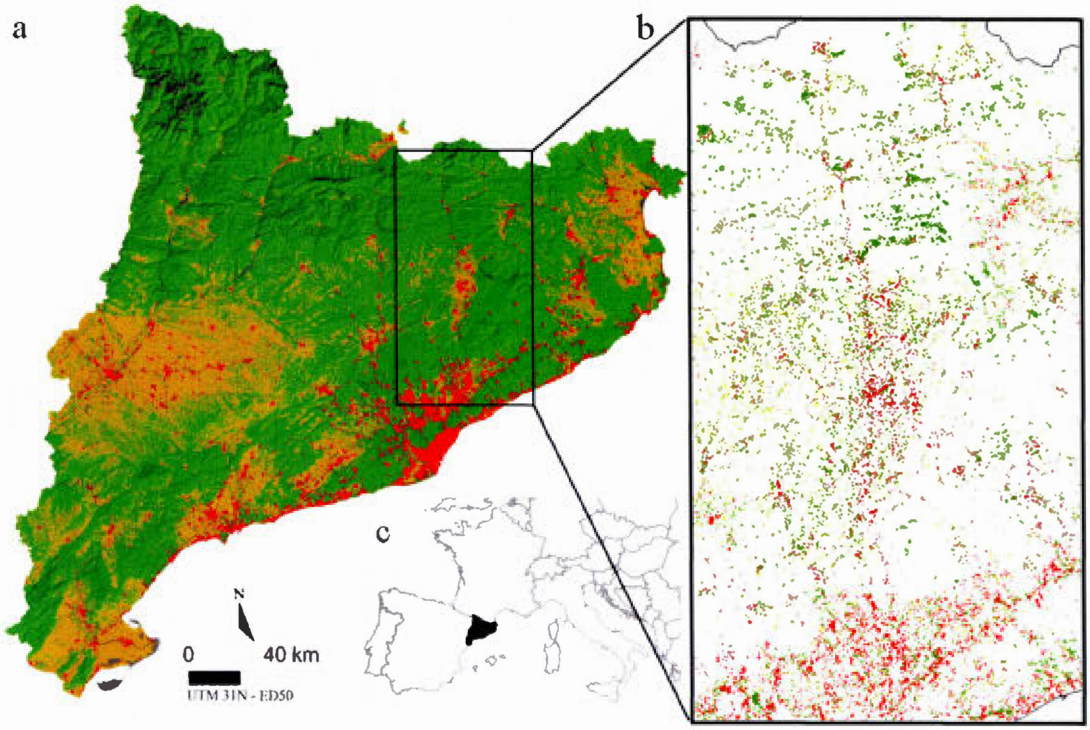

Figure 1.2: 2009 Land Cover Map of Catalonia (32 100 km^2) reclassified to four categories: urban in red, natural vegetation in green, agricultural land in yellow, and others in grey (a); zoom in for the land transitions observed between 1993 and 2009 in the northeastern part of Catalonia at 1 ha (b); and a situation map of Catalonia in the European context (c).

We evaluated the ability of the MEDLUC model to reproduce observed spatial patterns of change in Catalonia between 1993 and 2009 at 1 km^2 and 1 ha spatial resolutions. Since we were less interested in the spatial structure of changes and their biophysical and socio-economic drivers, we focused on evaluating the emerging patches-of-change distributions. We characterized the six empirical distributions of patches-of-change (i.e. urbanisation, rural abandonment, and agriculture expansion at 1 km^2 and 1 ha) as we did in the sensitivity analysis. First, we verified that empirical distributions could be approximated using a power law using the Vuong's test (implemented in the 'poweRlaw' R-package), a likelihood ratio test in which the null hypothesis is that the two compared distributions are equally far from the true distribution. After this verification, we determined the power-law β exponents of the observed distributions (β_{obs}) by fitting log-log linear regressions. Lastly, we calculated the four class metrics listed above for each distribution. We used the same combinatorial set of experiments described for the sensitivity analysis to calibrate the $\{\lambda_i, \lambda_s, k\}$ parameters. We ran 50 replicas of the model. The maximum likelihood parameter combinations were chosen based on the β exponent that best fitted the β_{obs} exponent (see Annex A for calibration details).

Because MEDLUC follows a demand-allocation approach, in each run the demand of any land transition was fully allocated. Thus, the generated maps were free of quantification error but not of location error (Pontius *et al.*, 2004), which came from the initialization of the *transition-potential* variable and the stochasticity of the allocation procedure (Equation 1 and 2). We carried out an error quantification test based on the percentage of cells correctly classified (Kuhnert *et al.*, 2005) and compared the predictive performance of MEDLUC with regard to a null model predicting absolute persistence (Pontius *et al.*, 2004). Specifically, we first produced the cross-tabulation analysis between the 1993 and 2009 versions of the Land Cover Map of Catalonia to retrieve the percentage of correct classifications (for each land-cover type) under the null model. We then averaged the percentage of correct classifications of the cross-tabulation analysis between each replica of the MEDLUC model and the 2009 reference map. Pontius *et al.* (2004) introduced the concept of null resolution, or the finest resolution at which the tested model performs as well as the null model. Therefore, we took the 50 LCT output maps of the maximum likelihood experiment at 1 ha and generalized at successive 2-fold coarser resolutions to repeated the same map-to-map comparisons.

1.4 Results

1.4.1 Sensitivity analysis of the demand-allocation procedure

The three model parameters $\{\lambda_i, \lambda_s, k\}$ of our procedure allowed reproducing a broad range of LULC spatial patterns (Table 1.2; Figures 1.3 and 1.4). Larger values of the rate of change occurrence λ_i increased the number of patches and decreased the maximum patch size (Table 1.2). That is, as λ_i increased patches started faster (i.e. closer in time) and they could not significantly grow in size (Figure 1.3). At higher rates of change-contagion λ_s, patches grew faster (Table 1.2) and fewer patches were needed to allocate the demand (Figure 1.3). The fractal dimension index measures the irregularity of patch shape: more complex perimeters results in index values equal or close to 2. In our framework, as patches increased in size they became more square-like in shape (Figure 1.3). By construction of the allocation procedure, the acceleration k amplified the effects of change contagion (Figure 1.3). Both λ_s and k positively interacted to allocate the demand in larger and more regular patches (Table 1.2). Nevertheless, the k parameter was not redundant because it allowed controlling change contagion in a non-linear way, thus broadening the variety of spatial patterns generated.

A detailed examination of the interaction between model parameters showed that for a high rate of change-occurrence ($\lambda_i = 20$) and a low change-contagion values ($\lambda_s = 0.1$), demand was always allocated in small scattered patches (i.e. power-law exponent had large values >1) (Figure 1.4, scenarios A1, B1, and C1). Distributions for these three scenarios had similar mean patch sizes, regardless of the value of k, but the largest patch was ca. 10-fold bigger for $k = 0.5$ than for $k = 0.1$ (Figure 1.4, scenarios A1 and C1). Thus, mean-equal distributions got fatter right tails depending on the change-contagion acceleration rate k. For the scenarios A2, B2, and C2 (with the same change-occurrence than the previous ones, $\lambda_i = 20$), because rate of contagion was 100-times bigger ($\lambda_s = 10$), change spreading was faster and patches could grow up before others started (Figure 1.4). When we only decreased the rate of patch occurrence to $\lambda_i = 0.25$ (i.e. scenarios A3, B3, and C3), spatial patterns lost their salt-and-pepper effect and demand was allocated in a few more regular patches. For these three scenarios (with $\lambda_i = 0.25$ and $\lambda_s = 10$) the β exponent got closer to 1 meaning that all patch sizes are equally represented (Figure 1.4). The effect of change-contagion acceleration was more evident at large λ_s (Figure 1.4): for all scenarios with $\lambda_s = 10$ (either with $\lambda_i = 20$ or $\lambda_i = 0.25$) the mean patch size roughly doubled when k increased from 0.1 to 0.3 (Figure 1.4, scenarios A2 - B2 and A3 - B3), and it roughly tripled when k went from 0.3 to 0.5 (Figure 1.4, scenarios B2 - C2 and B3 - C3).

Table 1.2: Estimates and F-values of the log-log regressions between the allocation parameters (and the two by two respective interactions) and the metrics characterizing patches-of-change distributions: the estimated slope of a power-law distribution (β), the number of patches per total demand (*nptch.dmnd*), the mean patch size (*mean.size*), the maximum patch size (*max.size*), and the maximum fractal dimension index (*max.frac.dim*) .

	β		nptch.dmnd		mean.size		max.size		max.frac.dim	
Factor	estimate	F	estimate	F	estimate	F	estimate	F	estimate	F
k	- 0.18	10 129	- 1.03	15 157	1.03	15 157	1.31	32 542	- 0.08	4 267
λ_i	0.02	7 971	0.14	5 130	- 0.14	5 130	- 0.03	3 282	0.01	2 043
λ_s	- 0.12	31 184	- 0.78	27 209	0.78	27 209	0.18	9 399	- 0.06	9 950
$k \times \lambda_i$	- 0.10	2 421	- 0.24	509	0.24	509	0.33	1 577	- 0.03	423
$k \times \lambda_s$	0.00	0.2	- 0.45	1 840	0.45	1 840	- 0.24	793	- 0.02	242
$\lambda_i \times \lambda_s$	0.01	308	0.09	527	- 0.09	527	- 0.01	13	0.01	191

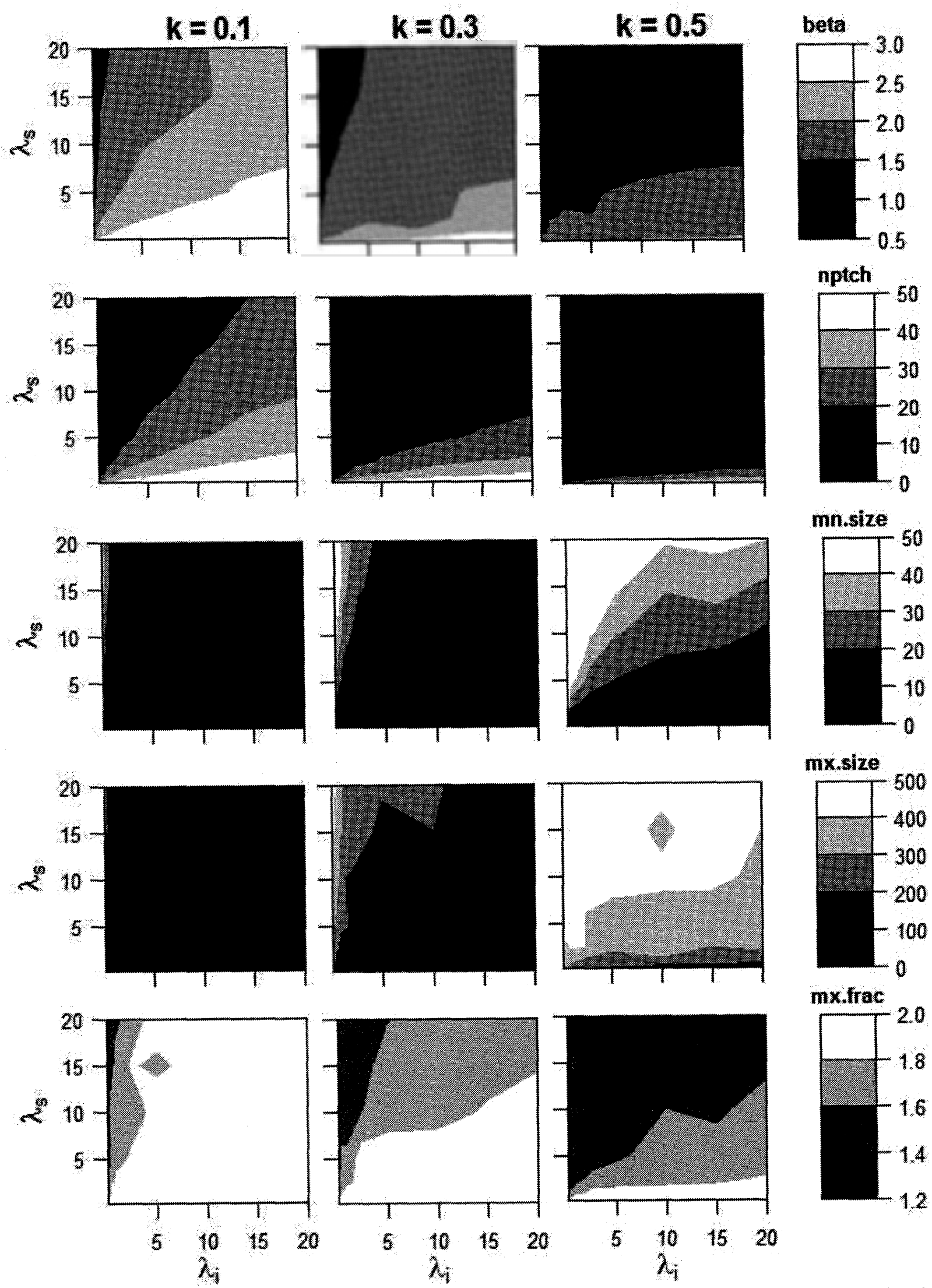

Figure 1.3: Contour plots of the estimated exponent of the power-law distribution (*beta*), the proportional number of patches to allocate a 100-pixel demand (*nptch*), the

mean patch size (*mn.size*), the maximum patch size (*mx.size*), and the maxim fractal dimension index (*mx.frac*) as a function of the model parameters λ_i (rate of land-use change origination) and λ_s (rate of land-use change contagion). In each column (from left to right) the model parameter k (intensity of contagion) takes value 0.1, 0.3, and 0.5 respectively.

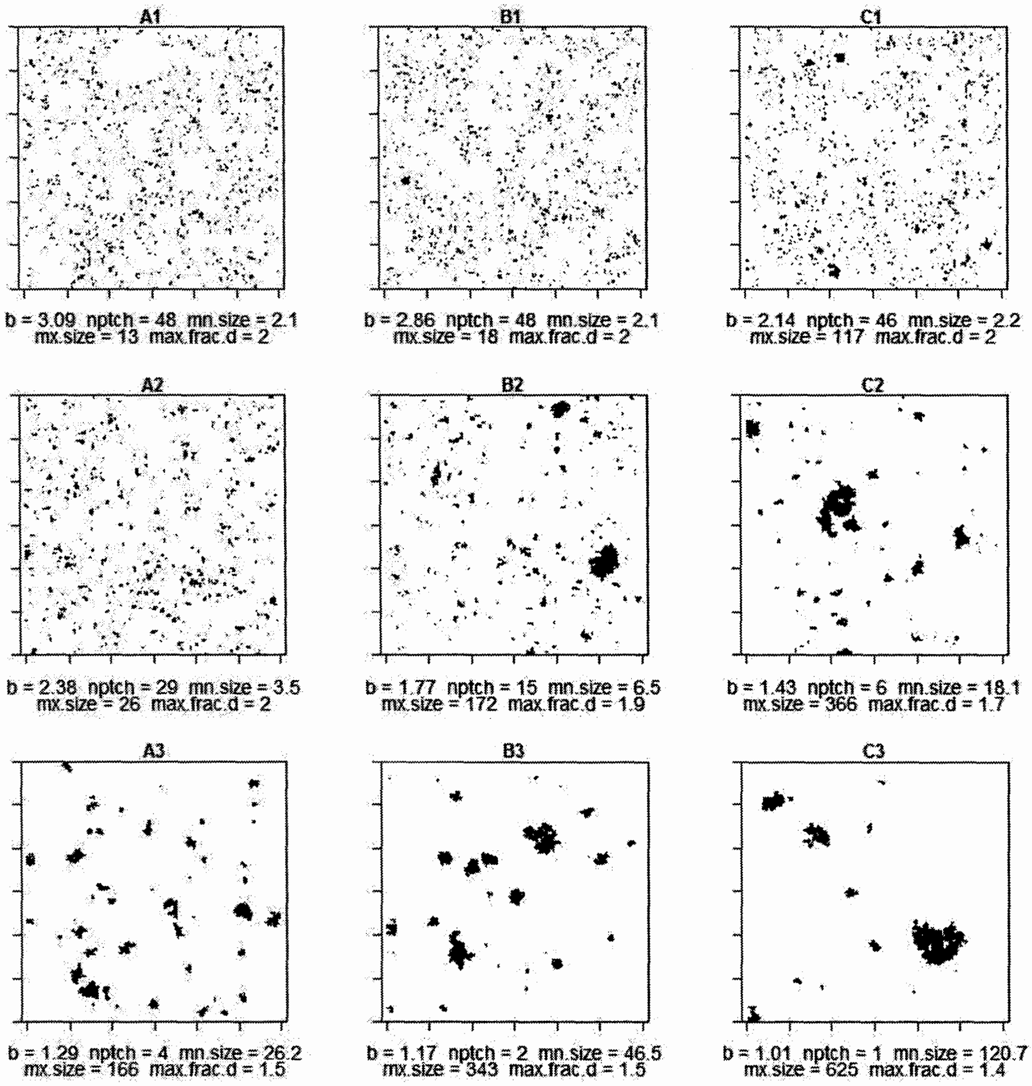

Figure 1.4: Patches of change generated by the demand-allocation procedure. One replicate for each of the nine selected scenarios is plotted. For these scenarios the $\{\lambda_i, \lambda_s, k\}$ parameters are A1 : {20, 0.1, 0.1}; B1 : {20, 0.1, 0.3}; C1 : {20, 0.1, 0.5}; A2 : {20, 10, 0.1}; B2 : {20, 10, 0.3}; C2 : {20, 10, 0.5}; A3 : {0.25, 10, 0.1}; B3 : {0.25, 10, 0.3}; C3 : {0.25, 10, 0.5} respectively. For each replica are given the estimated exponent of the power-law distribution (*b*), the proportional number of patches to allocate a 100-pixel demand (*nptch*), the mean patch size (*mn.size*), the maximum patch size (*mx.size*), and the maxim fractal dimension index (*mx.frac*). Plots' size is 180 km^2 and spatial resolution is 1 km.

1.4.2 Modelling LULC changes in a Mediterranean region

In the last two decades, agriculture expansion in the Mediterranean region of Catalonia has been a relatively rare process in terms of amount of change (Table 1.1) producing a scattered pattern of small patches-of-change (Table 1.3). Rural abandonment has been the most common transition in this region (Table 1.1), creating a spatial pattern dominated by relatively small patches-of-change but with a few contrasting large patches (Table 1.3). This pattern corresponds to the abandonment of marginal less-productive areas, but entire fields too (Baśnou *et al.*, 2013). Urbanisation is not negligible, 2.1% of territory has been converted to human-made amenities by the expansion of existing urban areas, the enlargement of road infrastructure, or the popping up of new homes and urbanisation in the wildland urban interface (Catalán *et al.*, 2008).

Patches-of-change size distributions for the for urbanisation, rural abandonment, and agriculture expansion observed in Catalonia between 1993 and 2009 followed a power law relationship when analyzed at both 1 km^2 and 1 ha spatial resolutions (*p*-value of the Vuong's test was 0.37, 0.96, and 0.44 for the distributions at 1 km^2 respectively, and 0.91, 0.80, and 0.91 at 1 ha respectively). Power-law relationships were scale-dependent for the three transitions (Table 1.3). All power-law exponents β were greater than 1, indicating that small patches accounted for most of the area that has undergone change.

The empirical urbanisation and rural abandonment processes generated similar patches-of-change distributions at 1 km^2, even if the distribution of urbanisation was evener (Table 1.3). Patches coming from rural abandonment were on average larger than those originated from urbanisation. In the study area, agriculture expansion mostly occurred in 1-cell patches, being the largest patch only 4 km^2. Fractal dimension was roughly constant for all transitions. Similar spatial patterns were observed when 1993 - 2009 land changes in Catalonia were analysed at 1 ha (Table 1.3), even if the magnitudes of change were not directly equivalent (Dietzel & Clarke, 2007; Kyle *et al.*, 2014).

At 1 km^2, the three transitions were successfully replicated when the change-contagion rate λ_s took relatively low values and the change-occurrence rate λ_i took high values (i.e. patches-of-change appeared concurrently). Emergent spatial patterns were dominated then by scattered, irregular, small patches, leading to β exponents greater than 1 (Table 1.4). The k change-contagion acceleration parameter increased from 0.1 for the agriculture expansion transition to 0.4 for the urbanisation and rural abandonment transitions. A lower k value reflected that agriculture expansion was mainly allocated in 1-cell patches. The modelled patches-of-change size distribution for urbanisation showed a longer right tail than the observed urbanisation distribution (Figure 1.5), meaning that the model produced a few large urban patches not observed in the studied period.

At 1 ha, the estimated $\{\lambda_i, \lambda_s, k\}$ parameter set generated patches-of-change distributions similar to the observed ones for the urbanisation and the rural abandonment transitions (Figure 1.5). However, on average, the largest patch modelled was 10- and 2-folds bigger than the observed largest patches respectively (Tables 1.3 and 1.4). The best fitting parameters for the agriculture expansion transition did not completely reproduce the empirical distribution (Figure 1.5).

Each simulation replicate generated a distinct spatial distribution of changes (Annex B). On average, the MEDLUC model performed better than the null model at 1 km^2 when allocating spatially new urban areas and new natural / semi-natural areas (Table 1.5). At 1 ha, the maximum likelihood parameterization of MEDLUC led to a percentage of correct classification higher than the null model when evaluating urbanisation, and still a good performance for allocating spatially rural abandonment (Table 1.5). At both resolutions, it failed at correctly allocating new agricultural patches (Table 1.5). The null resolution of MEDLUC predicting urbanisation and rural abandonment is 1 ha and 4 ha (cell size is 200 m) respectively, whereas it always performs worst than the null model when estimating agriculture expansion unless at a resolution 256 times coarser (Figure 1.6).

Table 1.3: Power-law exponent β_{obs} of the patches-of-change size distribution of the three main land-cover transitions observed in Catalonia between 1993 and 2009, at 1 km^2 and 1 ha of spatial resolution. Probability density functions were logarithmically transformed, and adjusted R^2 is for the slope parameter β_{obs} fitted by linear regression. For each land-cover transition, are provided the relative number of patches to allocate a 100-pixels demand (nptch.dmnd), the mean patch size and the standard deviation in brackets (*ptch.size*), the maximum patch size (*max.size*), the mean fractal dimension index and the standard deviation in brackets (*frac.dim*), and the maximum fractal dimension index (*max.frac*).

		β_{obs}	adj R^2	nptch.dmnd	patch.size	max.size	frac.dim	max.frac
1 km^2	Urbanization	2.5	0.99	49	2.1 (2)	15	1.5 (0.3)	2
	Rural abandonment	2.9	0.99	54	1.9 (0.4)	26	1.5 (0.3)	2
	Agriculture expansion	4.2	1.00	88	1.1 (2.1)	4	1.4 (0.4)	2
1 ha	Urbanization	2.3	0.99	21	4.7 (14.3)	637	1.4 (0.3)	2
	Rural abandonment	2.7	0.99	35	2.8 (7.1)	662	1.5 (0.3)	2
	Agriculture expansion	3.2	0.99	58	1.7 (2.3)	78	1.4 (0.3)	2

Table 1.4: Calibration results for the three land-cover transitions modeled in Catalonia between 1993 and 2009 at 1 km^2 and 1 ha. The set of parameters {λ_i, λ_s, k} is given for the experiment that generates the patches-of-change distribution that in average minimize the difference between the estimated and the observed probability density functions. For these experiments are given the estimated power law β_{est} parameter for the mean probability density function of the patches-of-change size distribution, the relative number of patches to allocate a 100-pixels demand (*nptch.dmnd*), the mean patch size (*mean.size*), the maximum patch size (*max.size*), and the mean fractal dimension index (*mean.frac.dim*). Metrics are averaged over the 20 model's replicas except for the maximum patch size metric that the median is assessed.

		$\{\lambda_i, \lambda_s, k\}$	β_{est}	nptch.dmnd	mean.size	max.size	mean. frac.dim
1 km^2	Urbanization	{15, 0.05, 0.4}	2.5	45	2.2	20	1.4
	Rural abandonment	{20, 0.1, 0.4}	3.1	61	1.6	10	1.4
	Agriculture expansion	{15, 0.25, 0.1}	4.2	89	1.1	3	1.3
1 ha	Urbanization	{10, 0.5, 0.5}	2.3	27	3.8	6 478	1.3
	Rural abandonment	{1, 0.05, 0.5}	2.6	41	2.4	1 320	1.4
	Agriculture expansion	{2.5, 0.1, 0.3}	3.3	71	1.4	33	1.3

Table 1.5: Percentage of cells correctly classified as urban, natural and semi-natural vegetation, agricultural land, and other land-cover types (water bodies and bare soil) by the null model and the MEDLUC model at 1 km^2 and 1 ha spatial resolution.

Land-cover types	1 km^2			1 ha		
	Null model	MEDLUC	difference	Null model	MEDLUC	difference
Urban	53	65	12	57	62	5
Natural, semi-natural	93	94	1	91	89	-2
Agricultural land	99	88	-11	96	81	-15
Others	72	72	0	62	62	0

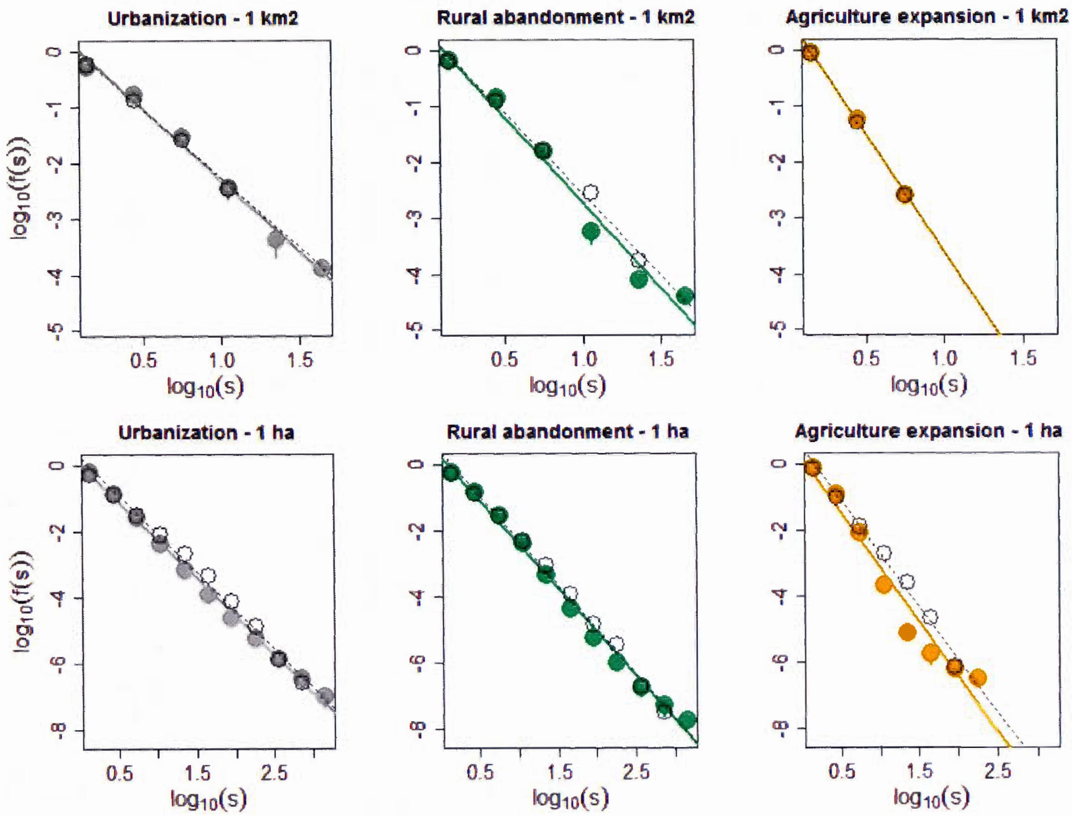

Figure 1.5: Probability density functions in a log-log scale for the patches-of-change size distributions at 1 km^2 and at 1 ha of spatial resolution for the three main land-use/cover transitions occurred in Catalonia from 1993 to 2009. Each panel shows the empirical probability density (empty black dots) and the distribution of the maximum likelihood experiment simulated by MEDLUC (full grey dots).

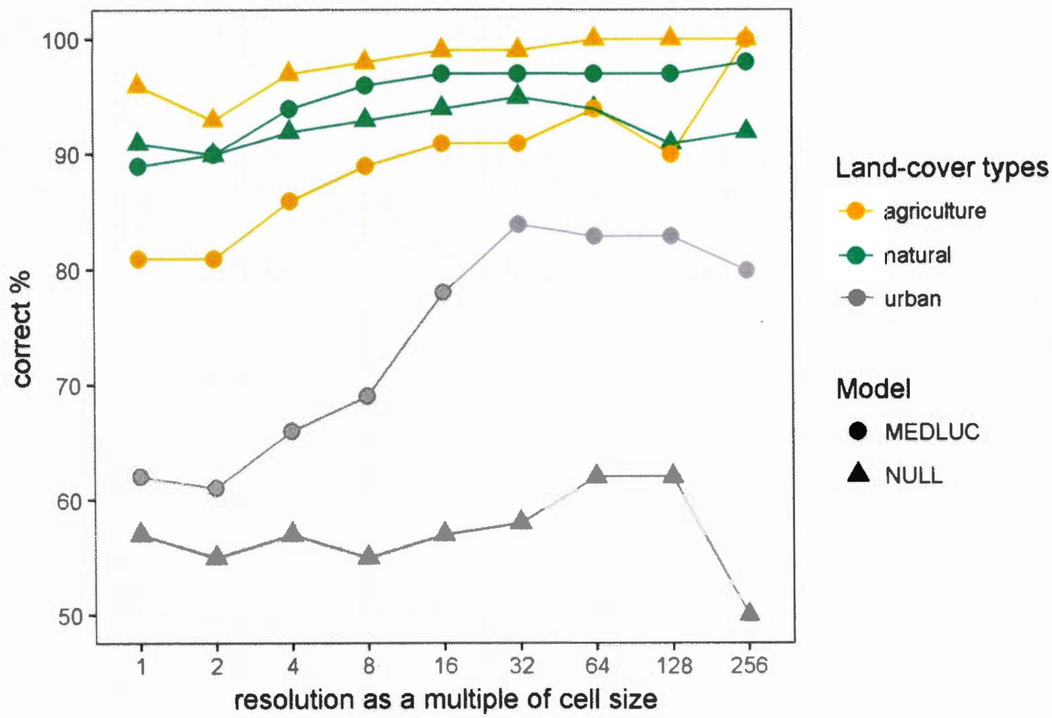

Figure 1.6: Percentage correct for three dynamic land-cover types (urban, natural and semi-natural lands, and agriculture) given by the Null model: the 1993 and 2009 versions of the Land Cover Map of Catalonia are cell-by-cell compared at 1 ha and at multiple coarser resolutions. The mean percentages correct of the MEDLUC model correspond to the maximum likelihood scenario initially run at 1 ha and further generalized at multiple coarser resolutions. The mean percentages are averaged over 50 runs.

1.5 Discussion

1.5.1 Strengths and limitations of the spatially demand-allocation procedure

We have shown here that a simple allocation rule (i.e. apply the LCT transition to the cell with the lowest time of a queue of active cells) depending on three parameters (i.e. the rate of change occurrence, the rate of change contagion, and the acceleration of such contagion) allows generating a vast array of spatial patterns of change (Figure 1.4). Yet, for each $\{\lambda_i, \lambda_s, k\}$ combination not a single, deterministic result emerges from the allocation-procedure. Since the processing times of the *initiating cells* and the *spreading cells* are stochastic (i.e. its value is drawn from an exponential distribution of rate λ_i and λ_s respectively), a distinct spatial distribution of changes arises each time the procedure is run (Figure 1.1). In our two implementations of the allocation procedure (for the sensitivity analysis and for replicating empirical land-transitions), the three parameters $\{\lambda_i, \lambda_s, k\}$ were always constant in time and did not depend on spatial variables. However, one possible extension of the proposed allocation strategy would be to use explanatory factors to modulate allocation parameters across space or in time, if the drivers that influence change occurrence or change contagion rates are known.

In the proposed modelling framework, the *transition-potential* variable influences the spatial distribution of new patches but does not affect change contagion. To include spatial constrains in change contagion, one could define a binary mask f_{lct} for each LCT transitions and include this new term in Equation 2. This modelling decision aims at differentiating biophysical or socio-economic factors influencing where LULC changes tend to occur from drivers of change determining aggregation patterns. The contagion of a land transformation from the first changed location to its neighbours is not necessarily led by these same primary biophysical or socio-economic factors, but often is a common feature to that transition. For example, wildland urban interfaces have been developed in extensive areas with similar environmental characteristics, but house agglomeration differs from region to region (Radeloff & Hammer, 2005). A purely empiric regression model would probably fail to allocate housing units following a specific sparse pattern. Our approach allows differentiating between the spatial configuration derived from expansive processes (e.g. urban sprawl) vs. consolidation processes (e.g. urban areas build up), as observed in Mediterranean landscapes (Catalán *et al.*, 2008).

Our demand-allocation approach is applicable to simulate more than one transition at a time. Because the land transitions of a socio-ecological system are beforehand explicitly defined, a LCT can feed multiple transitions, which can lead to spatial allocation conflicts. Competition for locations can be mainly addressed from two perspectives: imposing a temporal hierarchy or allowing competition for the most preferable locations (Verburg *et al.*, 2002; Rounsevell *et al.*, 2006b). Because only three land transitions of extremely different nature were modelled, an intuitive hierarchy was imposed in the current MEDLUC version. Nevertheless, the proposed framework has been built to allow land transitions to expand concurrently and compete for space according to their *transition-potential* variable and allocation parameters. If two transitions have identical land requirements, patches-of-change will potentially emerge in close locations but only one transition will effectively spread, the one with the faster occurrence and contagion rates (i.e. whose competitive advantage is higher). That is because the allocation procedure was designed to prevent more than one transition occurring at any location within a single time step. On the other hand, if the model is used dynamically (i.e. at least two time steps are simulated), then it is mandatory to establish the minimum sojourn time per land-transition, understood as the time before a cell can change state again. Because the modelling framework records the time since the last change, it tracks the locations available to change for any land-transition. If the minimum sojourn time is unknown, the most conservative approach is to set it at 0 (i.e. a transformed location will never change again).

We calibrated the MEDLUC model to emulate the spatial patterns of LULC change observed in Catalonia at 1 km^2 and 1 ha. Our calibration strategy focused on finding the parameter combinations that allowed replicating the general shape of the three empirical power-law distributions (but see Annex B), even if in general the model produced fatter right tails at both studied scales (Figure 1.5). If required, a practical (top-down) solution may be to stop the contagion process when a user-defined threshold is exceeded or when the patch grows over a fixed landscape percentage. In addition, we compared the performance to correctly allocate transitions of MEDLUC with that of a null model. The null model, that by definition predicted a perfect persistence of any LCT, returned a higher percentage match than MEDLUC when simulating agriculture conversion of the 1993-2009 period (Figure 1.6). Because this transition is relatively rare in the study area (Table 1.1) and the area allowed to change represented 62% of the territory, the model could not capture the right locations of new agriculture areas with a *transition-potential* variable only based on the spatial distribution of agriculture in 1993. In this case, other biophysical or socio-economical drivers behind this transition should be incorporated in these variable. On the other hand, that the MEDLUC (using a *transition-potential* exclusively defined according to the spatial distribution of the target LCT per transition) performed better than the null model for urbanisation and rural abandonment, highlights the relevance of landscape configuration itself on influencing LULC change processes (Verburg *et al.*, 2004; Dendoncker *et al.*, 2007).

1.5.2 *Comparison with other demand-allocation approaches*

The proposed allocation procedure assumes that land transitions occur in two phases: (1) change occurrence and (2) the spatial spreading of this change. The algorithm first selects multiple source cells from which patches-of-change will concurrently emerge, and then simulates transition contagion from source cells to their closest neighbours. This design is conceptually analogous to that adopted for modelling frameworks dealing with self-organising processes. Such approaches emulate the ignition events followed by the spatial spreading-like process; like forest fires and diseases (Rhodes & Anderson, 1998; Hargrove, 2000; Reed & McKelvey, 2002). The methodological design of our allocation procedure closely followed the CA philosophy: generate emergent spatial patterns from simple rules, in discrete time steps, over a landscape depicted by discrete cell states. But, instead of these rules being defined at the cell level, were defined at the transition (or process) level. In the CA approach, the likelihood of a cell to change state is function of a set of transition rules (and probabilities) and the state of neighbouring cells. Both the shape and size of the neighbourhood and its influence on central cell's state are mostly defined according to system's expert knowledge (White & Engelen, 2000). With our procedure we purposely reduced expert knowledge requirements and showed that a framework based on one rule is enough to generate reliable patterns of change. Indeed, the rule of "the cell with the minimum processing time (T_{ini} or T_{sprd}) changes" is valid for any land transition modelled (with different transition rates λ_i, λ_s, k to capture each process) (Figure 1.1). At the computational level, in a standard CA, at each time step all cells and their neighbourhoods are evaluated once (either sequentially or randomly), while in our procedure no more than $9 \times D^t_{lulc.trans}$ cells (per land transition) while be evaluated and ordered in the ascending-order queue (Figure 1.1).

Other spatially explicit LULC change models also recognize the complex dynamics of LULC change processes and separately address different phases (or components) of a land transition. The SLEUTH urban growth model is a CA-based model that incorporates four rules (spontaneous growth, breeding of a new urban core, urban expansion, and growth influenced by roads) to mimic different types of urban expansion patterns, such as isolated houses creation, urban centres consolidation, or urban sprawl (Clarke *et al.*, 1997, 2007). SLEUTH rules are based on four drivers of urban growth, namely land cover, slope, transportation network, and protected areas (Clarke *et al.*, 1997). Even if the model has been successfully world-wide used to mainly model urban expansion (Clarke *et al.*, 2007), these *a priori* rules limit its generality to any region with other rules or set of factors driving urbanisation, such as distance to the coast, regional economic development, or the presence of touristic attractions (e.g. ski resorts, lakes). It is worth mentioning that a recent extension of SLEUTH incorporating a probability map based on other biophysical and socio-economic drivers enhanced model performance (Rienow & Goetzke, 2015). Our new LULC modelling framework has not been as widely applied (and calibrated for different regions with specific datasets) as SLEUTH, but it was a priori designed to (1) model more than one land-transition at a time, (2) include all the potential drivers of LULC change for each transition independently of model structure, and (3) acknowledge the time and path dependence of LULC changes while defining a straightforward rule for any transition.

Another LULC change model taking into account neighbourhood influence on transitions probabilities is DINAMICA, which simulates deforestation and reforestation (from regrowing areas to mature forests) combining two spatial functions (Soares-Filho *et al.*, 2002). At each time step, DINAMICA assesses the demand from LCT i to LCT j as a function of a transition rate and the composition of the landscape. The demand will be truncated to guarantee a minimum occupation of

LCT *i*. In our modelling framework, effective demand emerges from the availability of land to be converted to the target LCT. Note that DINAMICA does not allow land transitions from multiple LCT to a target one, but each transition happens between a pair of LCTs, the source and the sink. In contrast, in our approach the same process can model more than one transition (e.g. urbanisation converts both natural and agricultural areas to urban ones). The first DINAMICA spatial transitional function simulates the expansion of a previous LCT patch, while the second generates new patches from seeds (Soares-Filho *et al.*, 2002). The demand of transition from LCT *i* to *j* is always divided in two proportional parts by the user, each one to be allocated by one of these functions. Despite the modelling approach is different, combinations of the rates λ_i, λ_s, and k also govern new patches creation and expansion (via spreading) of existing ones with less top-down control on the amount of change allocated in each phase. Yet, we did not control the mean size of new patches, while in DINAMICA patches of each LCT follow a user-specified lognormal distribution.

When a spatially explicit LULC change model simulates transitions occurring in parallel, a cell can be eventually claimed for multiple new land uses at the same time. Here we defined a sequential hierarchy of transitions, but this approach may not be suitable to simulate other situations, such as multiple agriculture conversion processes to different types of crops. In the CLUE model, competition for a location is solved by iteration (Verburg *et al.*, 2002). Until the demand of each land transitions is not fulfilled, locations that can feed more than one transition will more likely change to meet the more demanding transition. The CA_MARKOV model integrated in Idrisi software allocates changes according to a set of suitability maps (one per LCT), and if conflict arises in a cell it uses an algorithm based on a minimum-distance-to-ideal-point rule and weighted rank to determine the definitive LCT (Eastman, 2003). In our procedure, because the cells in the queue are ordered by processing time, the proposal of solving spatial competition by allowing all transitions to occur concurrently is conceptually logical (Section 1.5.1), but remains to be tested against alternative solutions in future applications.

1.5.3 Future land-use change scenarios

Our LULC change modelling framework is suitable to spatialize both normative and exploratory scenario storylines (Rounsevell & Metzger, 2010). By adopting the demand-allocation premise, our framework facilitates translating agricultural policies, urban development plans, or land management decisions following global trends or regional policies. But most important, it considers an explicit simple description of each specific land transition. These are fully determined by the spatial *transition-potential* to the new LCT and the spatial characterisation of change occurrence and spread. This avoids restricting (or enabling) transitions to locations that meet a priori set of conditions. Therefore, our modelling approach should be able to spatialize exploratory scenarios that substantially change the driving factors behind any LULC change process. Future urban and rural development policies applied in a region can explicitly envisage novel spatial patterns or emulate those observed in close regions, instead of being empirically constrained by the past (Ward *et al.*, 2000; Houet *et al.*, 2010). Our approach offers the alternative to predefine the spatial aggregation of land transitions, while artificial, non historically-based transition potentials can be used to allocate LULC changes (Overmars *et al.*, 2007).

1.6 Conclusions

Dividing land transitions in two phases, change occurrence and contagion, is still a poor exploited approach in LULC change modelling. Here, we recognized the self-organising, spreading nature of LULC changes. We succeeded in designing an algorithm that not only recognizes these two phases but proved to be enough simple, flexible, yet bottom-up to reproduce empirical patches-of-change distributions. Therefore, with this algorithm, we translated the focus from the spatial drivers of land-cover occurrence to the processes of change emergence and expansion. Multiple, scale-dependent factors and their corresponding spatio-temporal interactions are behind the occurrence and spreading of land transitions. Our modelling framework detaches where is more likely a LULC change occurs from the spatial process of change itself, but also allows overcoming limitations such as a poor knowledge of drivers or scarce data.

We applied the allocation procedure to replicated observed land-transitions in a Mediterranean region, while only relying on landscape configuration to initialize the variable accounting for the emergence likelihood of patches-of-change. Even if our calibration mainly focused on the generated patches-of-change distributions, we compared the performance of the MEDLUC model to that of a null model, finding that our model only failed at allocating the rarest and sparsest process of change (i.e. agriculture expansion). This simple initialization of the *potential-transition* variable, done without other biophysical or socio-economic drivers of change, allowed the model at least not performing worse than a null model for two transitions, urbanisation and rural abandonment.

The demand-allocation procedure proposed here is applicable to spatially translate scenarios of LULC change. However, as seen in our application in Catalonia at two spatial resolutions, even if the maximum likelihood parameter sets kept a proportional relation across them, it is not possible to extrapolate parameters fitted for one resolution to another. If the model needs to be applied at different scales or to another region, a calibration of the demand-allocation procedure is required for each scale. However, the modular structure of the LULC change model provided facilitates model calibration and validation, enabling potential users to focus on defining the demands, the transition potential maps, and the set of parameters driving LULC change emergence to extent it for any land transition of interest.

1.7 Acknowledgments

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CHAPTER II

THE POTENTIAL OF AGRICULTURAL CONVERSION TO SHAPE FOREST FIRE REGIMES IN FIRE-PRONE LANDSCAPES

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2.1 Abstract

In densely populated forest fire-prone landscapes, interactions between global change drivers have the potential of increasing the severity of natural disturbance regimes impacting forest ecosystems. Yet landscape mosaics play a crucial role in fire dynamics, recovering traditional agro-forest mosaics could mitigate the predicted increase on fire frequency and area affected by future fires. Here, we evaluated 24 landscape management scenarios that combine agricultural conversion and fire suppression as a means of reshaping future fire regimes. Scenarios differed in the rate of agricultural conversion, the spatial pattern (aggregate vs. scattered), and the location of new agricultural patches. To quantify the interactions between vegetation dynamics, fires, land-cover changes, and fire suppression we adopted a spatially explicit landscape dynamic meta-modelling approach by coupling a fire-succession model and a land-use/land-cover change model. Applied to a Mediterranean region, new landscape mosaics empowered fire-fighting extinction capacity only after 15 years (on average) of cumulative land transformations. An agricultural conversion of at least 100 $km^2 \cdot year^{-1}$ was required to significantly shape the fire regime. A conversion rate of 200 $km^2 \cdot year^{-1}$ substantially improved fire suppression effectiveness, but subsequent increases did not improve effectiveness. When aggregated, new agriculture patches contributed more effectively to fire reduction and decreased the edge effect on remaining forest patches. Agricultural conversion opens a new window for thoughtful long-term spatial planning aimed at minimizing the negative impacts of large wildfires on forest ecosystems. These alternative strategies could be used in other forest regions facing increasingly severe fire seasons to rethink their landscape management practices.

Keywords: Landscape management; Fire-succession model; Land-cover change model; Fire suppression; Agricultural conversion; Mediterranean

2.2 Introduction

Changing climatic conditions disrupt natural disturbance regimes affecting forest ecosystems (Dale *et al.*, 2001; Turner, 2010). In all biomes, the impacts of future fire regimes are more uncertain than ever because of climate change and its interaction with other global change components (Bergeron *et al.*, 2010; Bradstock, 2010; Batllori *et al.*, 2013; McKenzie & Littell, 2017). Globally, fire regimes are predicted to become more severe, more frequent, and to affect larger areas (Flannigan *et al.*, 2013). But at regional scales prediction of future fire incidence is not straightforward (Moritz *et al.*, 2012). Although the interrelationship between climate and vegetation partly explain fire incidence (Krawchuk & Moritz, 2011; Pausas & Ribeiro, 2013), in many regions of the world, human derived factors usually drive fire regimes (Bowman *et al.*, 2009; Archibald *et al.*, 2013; Knorr *et al.*, 2014). In coupled human-natural systems, fire regimes emerge from cross-scale and feedback interactions between fire ignitions, prevailing fire-weather conditions, landscape configuration, and fire suppression efforts. Lightning strikes are still the main cause of fires in remote areas (Stocks *et al.*, 2002), whereas human presence is behind most of fire ignitions worldwide (Ganteaume *et al.*, 2013; Hawbaker *et al.*, 2013). In humanized landscape mosaics, low fuel conditions and fuel discontinuity generated by active forest management, prescribed burnings, agricultural activities, or human-made infrastructures have the potential to strongly shape fire regimes (O'Donnell *et al.*, 2011; Collins *et al.*, 2015). However, even when landscape configuration and composition drive fire spread and intensity, fire impact still depends on fire-prone weather conditions, which actually determine the way in which fires "read" the landscape features and therefore respond to fuel discontinuities (Turner & Romme, 1994; Moreira *et al.*, 2011). Finally, fire suppression policies have usually advocated for a total fire exclusion, and due to the improvements in fire-fighter training, use of technology, and increased availability of economic resources, most fires are indeed successfully extinguished over a broad range of conditions (Donovan & Brown, 2005; Fernandes *et al.*, 2016). Therefore, a fire regime cannot be treated as a top-down external force driving forest ecosystems dynamics, but rather as an inherent, dynamic component of the human-natural system, tightly linked to the territory in which it occurs and the society it affects (Tedim *et al.*, 2016).

Land-use land-cover (LULC) change, identified as a major component of global change responds to socio-economic development and related activities (Lambin *et al.*, 2001). Increasing demands for energy, water, and food from a growing population will intensify the anthropogenic pressure on natural resources like forests (Foley *et al.*, 2005). In many countries, rapid deforestation processes, wildland-urban interface sprawl, plantations of both native and exotic species, agriculture intensification, or rural abandonment since the mid-20th century have transformed entire landscapes (Radeloff & Hammer, 2005; Rudel *et al.*, 2005; Navarro & Pereira, 2012). The side effects of such land cover changes on disturbance regimes such as fires are starting to be assessed but are difficult to anticipate. For example, urban sprawl into semi-natural land covers non-linearly increases the exposure to wildfires (Syphard *et al.*, 2007; Vilar *et al.*, 2016), while in fire-prone landscapes of southern Europe, both agriculture abandonment and afforestation have been associated to increases in fire activity (Moreira *et al.*, 2001; Viedma *et al.*, 2015). Yet, the compound cumulative impacts of LULC changes on fire regimes remain largely unknown. Large-scale human interventions (e.g. urban expansion, sylvicultural treatments, forest plantations, grazing, agriculture intensification) continuously reshape fuels loads and their spatial arrangement, thus destabilize the self-organization dynamics of fire regimes and the balancing feedback loops between fire-adapted forest ecosystems and wildfires (Moreira *et al.*, 2009; Vilar *et al.*, 2016).

Understanding the interactions between shifting disturbance regimes, global warming and LULC changes will allow us to anticipate undesirable impacts, as well as to estimate the results of specific management actions and policies (Doblas-Miranda *et al.*, 2015). In highly humanized fire-prone landscapes novel combinations of global change drivers are expected to influence ecosystems in unprecedented, often non-linear responses leading to new, emerging environmental in which the resilience of the system can be compromised (Johnstone *et al.*, 2016). The challenge lies here in building resilience-based forest management approaches that explicitly reduce vulnerability and exposure to known (and unknown) stressors (Chapin *et al.*, 2010). Because past outcomes do not ensure future success (Gustafson, 2013), the development of new approaches to estimate the effects of management actions and to capture the spatio-temporal dynamics of humanized fire-prone landscapes which incorporate the uncertainty related to global change are urgently needed (Hantson *et al.*, 2015). Non-correlative, process-based modelling approaches (1) combining multiple drivers of global change, (2) accounting for multi-scale interactions, and (3) explicitly dealing with uncertainty can be part of the solution. Models have to be scenario-oriented, spatially explicit, and incorporate fire behaviour and vegetation response to fire, but LULC changes (or forest management plans) and fire suppression too (IPBES, 2016). In particular, stakeholders and planners need a priori evaluation of the efficiency of fire-reduction strategies within a holistic context to provide (1) insights into the cumulative impacts of such policies on the land, (2) the potential time lag between the implementation and the benefits, and (3) any apparent long-term side effects on forest functioning.

Here, we assess the interactions between wildfire, LULC change, and landscape management actions (i.e. fire suppression) in a high fire risk, densely populated, forested Mediterranean region. We adopt a landscape dynamic meta-modelling approach, coupling two existing spatially explicit models, a fire-succession model

(Brotons *et al.*, 2013) and a LULC change model (Aquilué *et al.*, 2017). The resulting meta-model accounts for spatio-temporal interactions between fire ignitions, fire spread (that depends on landscape composition and species fire sensitivity), fire suppression, LULC transitions, and ecological processes (mainly post-fire regeneration and afforestation). We focus on examining alternative fire management strategies that seek to reduce vulnerability of forest landscapes to fires while preserving functionally rich forest. We propose a set of scenarios aimed at restoring the heterogeneity of past Mediterranean landscapes by allocating new croplands and pastures to current less fuel constrained landscapes (Pausas & Fernández-Muñoz, 2012). We then evaluate effectiveness of treatments by quantifying the area suppressed when using the discontinuities in the landscape in relation to the amount of area that had burnt if these would have not been present.

With the analyses of suppression effectiveness across a gradient of landscape heterogeneity, we aim at addressing two major research questions: (1) How will changing landscape configurations and active fire suppression reshape fire regimes in a fire-prone landscape, and (2) How will the forest cover spatial distribution be affected by cumulative conversions to agricultural land. The spatial arrangement and connectivity of fuels drive fire behaviour, but when connectivity is below a critical percolation threshold, fires are unlikely to spread and grow (Turner *et al.*, 2001). Indeed, fire spread patterns behave non-linearly close to that theoretical threshold (Hargrove, 2000; Miller & Urban, 2000; Loehle, 2004; Abades *et al.*, 2014). Therefore, we posit two contrasting hypotheses about non-linear responses of fire suppression effectiveness across the landscape heterogeneity gradient induced by agricultural land conversion (Figure 2.1). According to percolation theory, new agricultural patches can have a positive, non-linear effect on the fire extinction capacity because high burnable fuels will progressively become less connected. But we expect that this positive effect is likely to be specially weak in landscapes with low agricultural land, even if it is likely to become stronger as this land use is more abundant (Figure 2.1a). Conversely, in landscapes with already larger amounts of agricultural land, further agricultural conversion may have a disproportional effect on fire suppression effectiveness. Eventually, landscapes will slowly reach a maximum capacity of influencing the fire regime (Figure 2.1b).

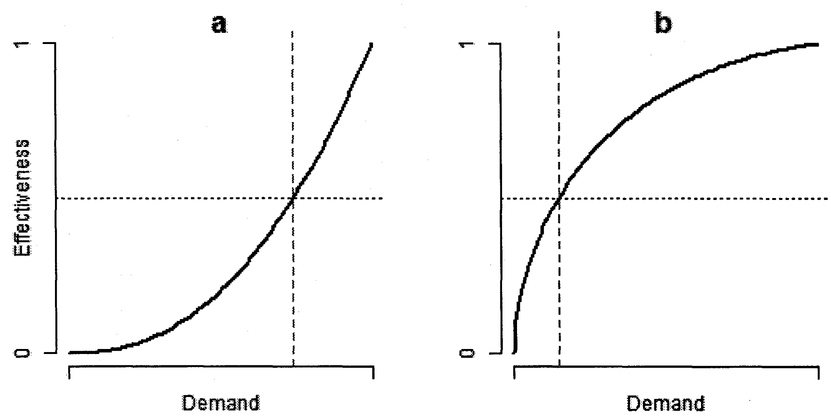

Figure 2.1: Two contrasting hypotheses about the non-linear relations between fire suppression effectiveness and the amount of agriculture allocated in the landscape (i.e. demand). Horizontal line is at 0.5 of effectiveness while the vertical line indicates the demand leading at 0.5 of effectiveness.

2.3 Methods

2.3.1 Study area

We use European Mediterranean ecosystems as relevant, highly humanized, fire-prone landscapes susceptible to irreversible transformations under global change (Verburg *et al.*, 2010; Batllori *et al.*, 2013). Climate warming and interacting anthropogenic factors both driving forest distribution and vegetation dynamics make Mediterranean Europe highly vulnerable to severe fire events (Moreira *et al.*, 2011; Moritz *et al.*, 2012; Doblas-Miranda *et al.*, 2015). In the last four-five decades southern Europe has experienced socio-economic transformations that have deeply altered traditional landscapes, mainly through the rural exodus from remote mountainous areas and the urban sprawl around cities and along the coasts (San Roman Sanz *et al.*, 2013; Stellmes *et al.*, 2013). Spatially continuous matrixes of relatively young forests with an abundant and dense understory now predominate in abandoned lands. Zero-fire suppression polices have led fuel loads build up even more (Tedim *et al.*, 2016) exacerbating the fire paradox: even if most of the fires get extinct, a few large events remain uncontrollable and catastrophic (González & Pukkala, 2007). However, in some regions, changes on forest landscape configuration have mitigate the favourable fire-weather conditions for intense and severe fire seasons (Fernandes *et al.*, 2014). This opens a management perspective to develop innovative fire-prevention policies in such densely populated fire-prone areas (Calkin *et al.*, 2015).

Catalonia was identified as a characteristic fire-prone Mediterranean region in NE Spain for applying alternative landscape management scenarios targeting the reduction of fire impacts (see Annex C for a full portrait). In Catalonia, wildfires are the main natural disturbance triggering most ecological processes and promoting landscape heterogeneity (Lloret *et al.*, 2002). Most of the ignitions are human-related, either accidentally or intentionally (González-Olabarria *et al.*, 2012). The systematic abandonment of traditional agricultural and farming activities during the last mid-20th century has translated into an unstructured rewilding of ancient croplands and pastures (Cervera *et al.*, 2016). Such recently established forests create homogeneous landscapes with fewer fire-breaks and present a fuel vertical continuity that facilitates the spread of crown fires (Lloret *et al.*, 2002). Moreover, since the dramatic 1994 and 1998 fire seasons in Catalonia, fire experts have devoted more efforts to understanding fire spread patterns according to synoptic conditions (Otero & Nielsen, 2017). Nowadays, fire brigades are better able to anticipate fire behaviour and achieve successful fire suppression.

2.3.2 The MEDFIRE, a fire-succession model

The MEDFIRE is a landscape dynamic model that integrates vegetation dynamics and fire regimes to investigate the interactions among ecological processes shaping Mediterranean landscapes (Brotons *et al.*, 2013). The fire regime is modelled by a top-down approach, in this case, the annual target area to be burned and the fire size distributions are model inputs (Annex D). In a given model run, the annual target area is burnt with as many fires (of a predefined target area) are needed. However, the spatial distribution of fires and the realized fire perimeters emerge from the interplay between the ignition probability and the landscape configuration itself (as both forest composition and fuel abundance play a key role). In the current version, fire ignition is a function of climate, road network, and landscape mosaic (Annex D). Fires spread following orography, main wind direction, and the most flammable fuels (Annex D).

Three main fire spread patterns have been identified for Catalonia: convective, topography-driven, and wind-driven fires (Duane *et al.*, 2016). Homogeneous fire regime zones are characterized by the proportion of fires that spread following each of the three patterns (Figure C.3). In the model, the fire spread pattern of a simulated fire is assigned according to the location of the ignition within a homogeneous fire regime zone.

In our approach, post-fire regeneration and afforestation are the two most relevant ecological processes inducing changes at the landscape scale. The first is modelled by a state-transition approach. Probability of regeneration depends on the previous state (pre-fire tree species) and the presence of potential colonizers within a 2 km circular neighbourhood. This means that only species in the surrounding area are allowed to establish in the recently burnt locations. This restriction avoids the situation of having communities not observed in the study area artificially emerge on the landscape. Transition probabilities are based on empirical data from Rodrigo *et al.*, (2004) and extrapolated to the study area by Brotons *et al.*, (2013). When many species form the pool of potential states for a specific transition (13 in the case of post-fire regeneration), a raw state-transition approach may lead to a spatially uncorrelated regeneration, particularly noticeable in large burnt areas. Because post-fire regeneration tends to occur in patchy patterns, c.a. 40 % of the burnt locations mimic the regeneration pathway of their neighbours: a burnt location randomly adopts the same state of one of its 8 neighbours whenever these have already changed state (Brotons *et al.*, 2013). The annual probability of scrubland colonization was calibrated as a logistic model of climatic, orographic, and forest explanatory variables (Annex D).

2.3.3 *The MEDLUC, a land-use land-cover change model*

The MEDLUC is a spatially explicit land-use land-cover change model designed to reproduce any LULC transition (Aquilué *et al.*, 2017). Given a LULC map with a few discrete categories, a land transition (e.g. urbanization) is the transformation of a subset of categories (e.g. forest, scrublands and croplands) to a target category (e.g. urban areas). The MEDLUC is based on a demand-allocation approach. That is, the demand or quantity-of-change is user defined, while the model spatially allocates that quantity into patches-of-change. The spatial distribution of changes is driven by a transition-potential map while the allocation of transitions occurs in two phases: origination and extension of land change. A triplet of parameters control both the speed of new patches-of-change origination and the speed of change aggregation around the first source cell (Annex D). A simple algorithm gives MEDLUC high flexibility to mimic a myriad of patterns of change (Aquilué *et al.*, 2017). The model has already been calibrated at 1 ha to reproduce the three main land transitions observed in Catalonia: urbanization, rural abandonment, and agricultural conversion (Aquilué *et al.*, 2017).

2.3.4 *Coupling fire and land-use change models*

We dynamically coupled the MEDFIRE and MEDLUC models to spatialize our scenarios, that is, to allocate new agricultural land on the landscape and observe how the fire regime responds. The models share the same set of state variables (land-cover, time since last fire, and time since last LULC change), and processes of both models are influenced by and update these state variables. In the current application, the main state variable, the land-cover / forest-species map describes the composition of the Catalan territory (Figure C.1). It details the distribution of the 12 most abundant tree species, scrublands, grasslands, and other main land-covers (arable land, permanent crops, urban areas, bare soil, and inland water). When coupling two models, all processes occur sequentially (either at uneven or regular time intervals), so the effects on the landscape accumulate. We configured the MEDFIRE time step at 1 year, while LULC changes occur every 5 years. Both models operate at the same spatial resolution of 1 ha.

The crucial first steps when coupling the two models was to identify the processes in one of the models affected by the changes in the state variables induced by the other model, and vice versa. The next step was to design the processes to capture the dynamics of the system. In our modelling framework, fire behaviour was the bridging process between MEDFIRE and MEDLUC. Fires were sensitive to new land-cover spatial mosaics through ignition probability and fire spread. Ignition probability was function of the neighbourhood configuration, and according to calibration was higher in urban-wildland interfaces and agro-forest landscapes (Annex D). Fire spread was function of tree species flammability, and following calibration, we were able to determine that fire fronts advance faster and at higher intensity when cross forests and scrublands rather than croplands (Annex D).

Whenever rural land abandonment or agricultural conversion processes occur, the newly generated semi-natural or agricultural patches, respectively, had to be integrated into the fire-succession model dynamics. Recently abandoned fields above an elevation of 1500 m were converted to alpine grasslands, otherwise became scrublands. The probability of being colonized by tree species increased with time, as for burnt scrublands. Scrublands and forests converted to agricultural land became either arable land (extensive cereals) or permanent crops (orchards) following a neighbouring rule that looks at the predominant type of agricultural land within a 500 m radius. None of the LULC change processes (urbanization, rural abandonment, and agricultural conversion) were influenced by either fire impacts or vegetation dynamics.

2.3.5 A fire suppression strategy sensitive to landscape configuration

For this study, we were particularly interested in fire suppression strategies responsive to changes in landscape configuration. The aim here was to build a strategy that used agricultural patches as landscape opportunities to start fire suppression. We focused on the continuity of agricultural land (i.e. on detecting patches rather than isolated cells) to provide areas that are open enough to enable fire fighters to get close to the fire front. To implement this strategy, all advancing fire fronts of a growing fire recorded the amount of agricultural area burnt in their neighbourhood (understanding that two locations are contiguous if they share at least one vertex). Then, a suppression rule was established: when a fire front had already burnt in continuity *Th* ha of agriculture, suppression was activated. Hence, any future cell reached by that fire front would not effectively burn, whereas the target fire area would decrease anyways (Figure 2.2). The level of suppression was defined by the threshold *Th;* as *Th* decreases, the smaller the patch of agricultural land is required to start the suppression, and the stronger the contribution of this land type to halting advancing fronts (Figure 2.2).

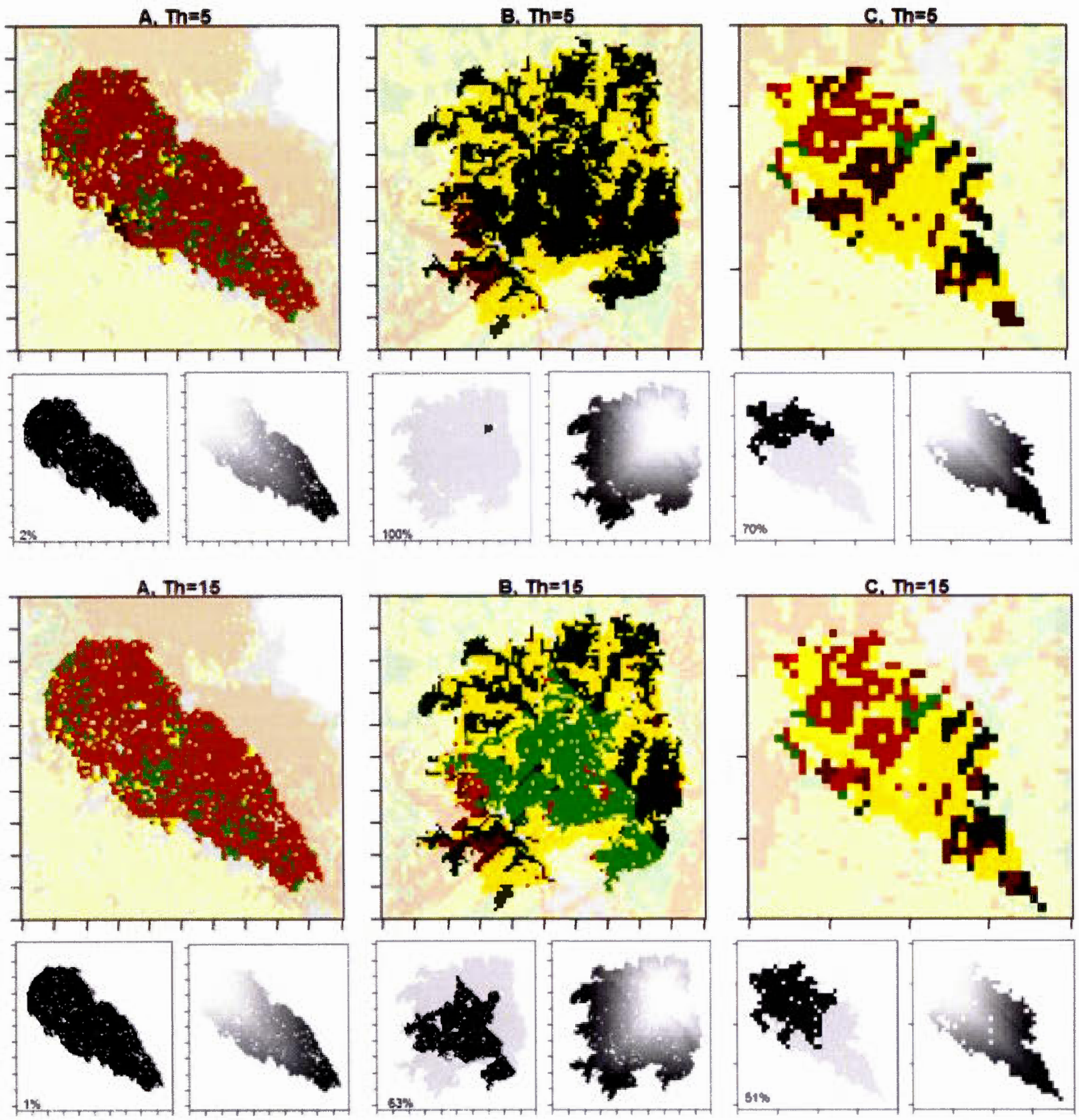

Figure 2.2: Two wind-driven fires (A and C) and one convective fire (B) suppressed at high and low levels of suppression (*Th* = 5 and 15 ha, respectively). For each fire, the upper panel shows the land-cover types: (1) non burnt (crop - yellow, green - forest, brown - shrub, grey - urban in pastel), (2) burnt (same colour code but darker), and (3) suppressed (same colour code but even darker). The lower left panel shows the total burnt (black) and suppressed (light grey) area with the ignition point (dark grey). The lower right panel shows the progression of the fire front (from light grey to

black). Spatial resolution is 1 ha. The length of plots A and B is 100 cells, and plot C is 40 cells. The value in the lower left panel indicates the percentage of suppressed area. Fire suppression is barely activated in the 3000 ha wind-driven fire (A) at both thresholds because fire front advances in high intensity across scrublands and forest, burning them. The convective fire (B) is completely suppressed when *Th* is 5 ha (because the ignition point is located in the middle of an agricultural patch) but when the suppression is weaker (*Th* = 15 ha), the suppressed area is reduced to 63%. The 500 ha wind-driven fire (C) clearly benefits from the agricultural area impeding the fire advance.

2.3.6 Landscape management scenarios

Three alternative landscape management strategies were considered in accordance with potential public policies regarding land management in fire-prone landscapes. The aim of all strategies was to increase current agricultural area. Each strategy was characterized by a transition-potential map that prioritized where allocate new croplands (Figure 2.3). The Fire Management (FM) strategy assumed a specific interest in managing land for fire prevention. Thus, new croplands were located in high fire risk areas (Equation D.4). The Rural Development (RD) strategy related to policies for boosting the economy of marginal areas that were likely the target of past rural abandonment processes. Zones mostly covered by young forests and scrublands were prioritized to undergone change (Equation D.5). The Crop Productivity (CP) strategy was like a business-as-usual scenario, where new agricultural land was placed close to the current productive areas (Equation D.6). The transition-potential maps were indeed updated over time as natural areas progressively transform to agricultural areas (Equations D.4, D.5, and D.6).

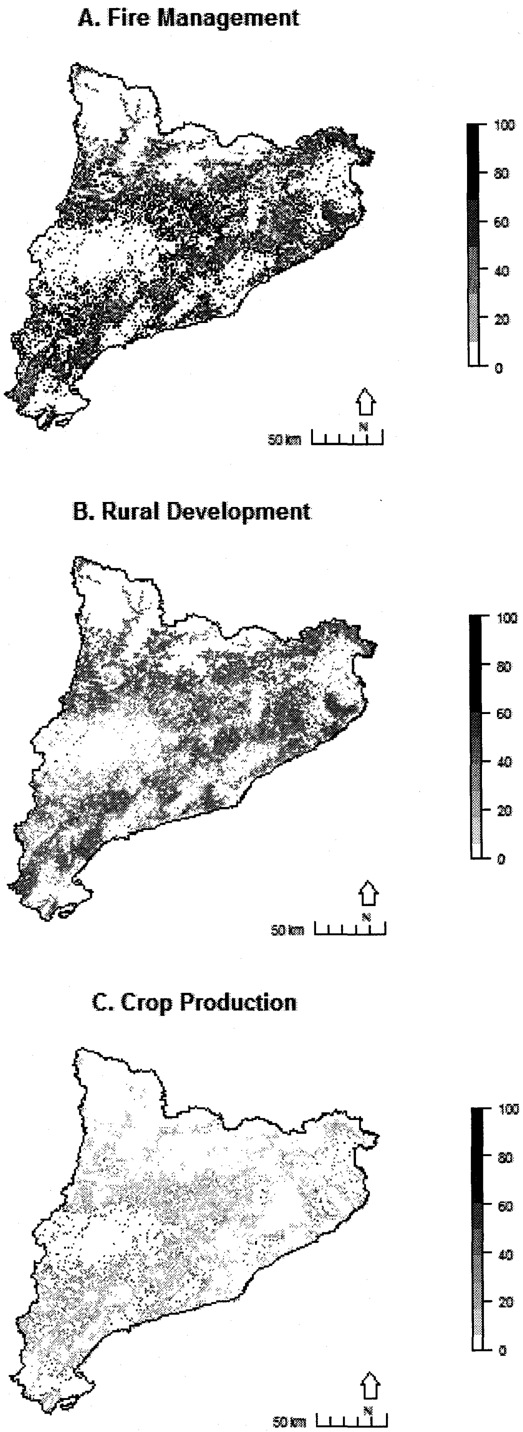

Figure 2.3: Initial transition-potential map (year 2010) for the Fire Management (A), Rural Development (B), and Crop Production (C) storyline, respectively.

We created a factorial design to investigate how much, where, and under which spatial pattern agricultural conversion influenced fire regime (Table 2.1). All three strategies were tested with a certain level of demand of new agricultural land to be allocated, either following an aggregate (AGG) or a scattered (SCA) pattern (Figure D.2). The observed rural abandonment rate was used to set the demand for agricultural conversion, as a means to reverse the past trend. In Catalonia, in a 16-year period, 1599 km^2 were abandoned, that is ca. 100 $km^2 \cdot year^{-1}$ (CREAF, 2009). We decided to test four agricultural annual demands: D2 = 50, D = 100, 2D = 200, and 3D = 300 $km^2 \cdot year^{-1}$ (Table 1). As the MEDLUC time step was set at 5 years, the demands actually allocated by the model were five times those mentioned above (however, for clarity we will continue to refer to these annual rates of agricultural land conversion). In all scenarios, urbanization took place at half of the observed rate, that is 21.5 $km^2 \cdot year^{-1}$ (CREAF, 2009). A control scenario was set at this same rate to simulate only urbanization. Each scenario (3 strategies × 4 demands × 2 spatial patterns + 1 control = 25 in total) was run 30 times for a 40-year period, from 2011 to 2050 inclusively. Because LULC changes occurred every 5 years, the landscape composition was untouched for the first period, from 2011 to 2015.

2.3.7 Analysis of scenarios

To quantify the effects of LULC changes on the fire regime over time, we measured three indicators in each scenario: (1) effectiveness, defined as the ratio at the fire level of suppressed area to target fire area, (2) leverage, or the amount of suppressed area in relation to the area transformed to agricultural land, and (3) the percentage of large fires (≥ 500 ha). All three variables were assessed every 5 years, at the end of the 40-year period, and for the last 20 years (from 2031 to 2050). We tested the significance of our scenarios with two ANCOVA analyses. We split the scenarios (Table 2.1) according to the spatial pattern (AGG or SCA), set the demand as the continuous variable, and the strategy (FM, RD, or CP) as the categorical variable. We determined whether the scenarios performed as well as or better than the control scenario by comparing effectiveness distributions 2-by-2 with a Wilcox test. We also verified if effectiveness improved over time by comparing the first 5-year period benefiting from changes in landscape composition, the 2016 - 2020 sub-period, with subsequent 5-year periods. To quantify the effects of LULC changes on forests, we characterized the spatial distribution of forests at the end of the period by measuring the mean patch core area and the mean shape index at the *vegueria* level (an administrative - biogeographic division of the Catalan territory, Figure C.5). The shape index measures the complexity of the patch shape comparing its perimeter with that of a square of the same size. It is independent of patch size and increases from 1 for the most compact squared patch as patch shape becomes more irregular.

Table 2.1: Identification codes for the 24 landscape management scenarios that identify the strategy, the level of demand, and the spatial pattern for new agricultural land.

Scenarios	Strategies	Demand ($km^2 \cdot y^{-1}$)	Spatial pattern
CP_D2_AGG	Crop Productivity (CP)	50 (D2)	Aggregate (AGG)
CP_D2_SCA			Scattered (SCA)
CP_D_AGG		100 (D)	Aggregate
CP_D_SCA			Scattered
CP_2D_AGG		200 (2D)	Aggregate
CP_2D_SCA			Scattered
CP_3D_AGG		300 (3D)	Aggregate
CP_3D_SCA			Scattered
FM_D2_AGG	Fire Management (FM)	50	Aggregate
FM_D2_SCA			Scattered
FM_D_AGG		100	Aggregate
FM_D_SCA			Scattered
FM_2D_AGG		200	Aggregate
FM_2D_SCA			Scattered
FM_3D_AGG		300	Aggregate
FM_3D_SCA			Scattered
RD_D2_AGG	Rural Development (RD)	50	Aggregate
RD_D2_SCA			Scattered
RD_D_AGG		100	Aggregate
RD_D_SCA			Scattered
RD_2D_AGG		200	Aggregate
RD_2D_SCA			Scattered
RD_3D_AGG		300	Aggregate
RD_3D_SCA			Scattered

2.4 Results

Fire suppression effectiveness increased with conversion to agricultural land, but not always linearly (Figures 2.4a and 2.5). For scenarios with a low demand of agricultural land conversion (D2 and D), effectiveness remained almost constant over the entire period, except for the FM strategy, where it was slightly higher at the end of the period for the D scenario (Figure 2.5). For higher demands (2D and 3D), RD scenarios showed a linear increase in fire suppression effectiveness over time when spatial patterns were scattered, but a rapidly saturating effectiveness when spatial patterns were aggregated (Figure 2.5). This saturation behaviour applies for most FM scenarios. Although fire suppression effectiveness increased over time for most of the scenarios, a minimum amount of time was required to observe a significant increment (Table 2.2). Low demand scenarios (D2 and D) needed on average twice as much time as high demand scenarios (2D and 3D) to show an increase in fire suppression effectiveness (Table 2.2). Thus, land-cover changes need to take hold in the landscape before having a significant impact on the fire regime.

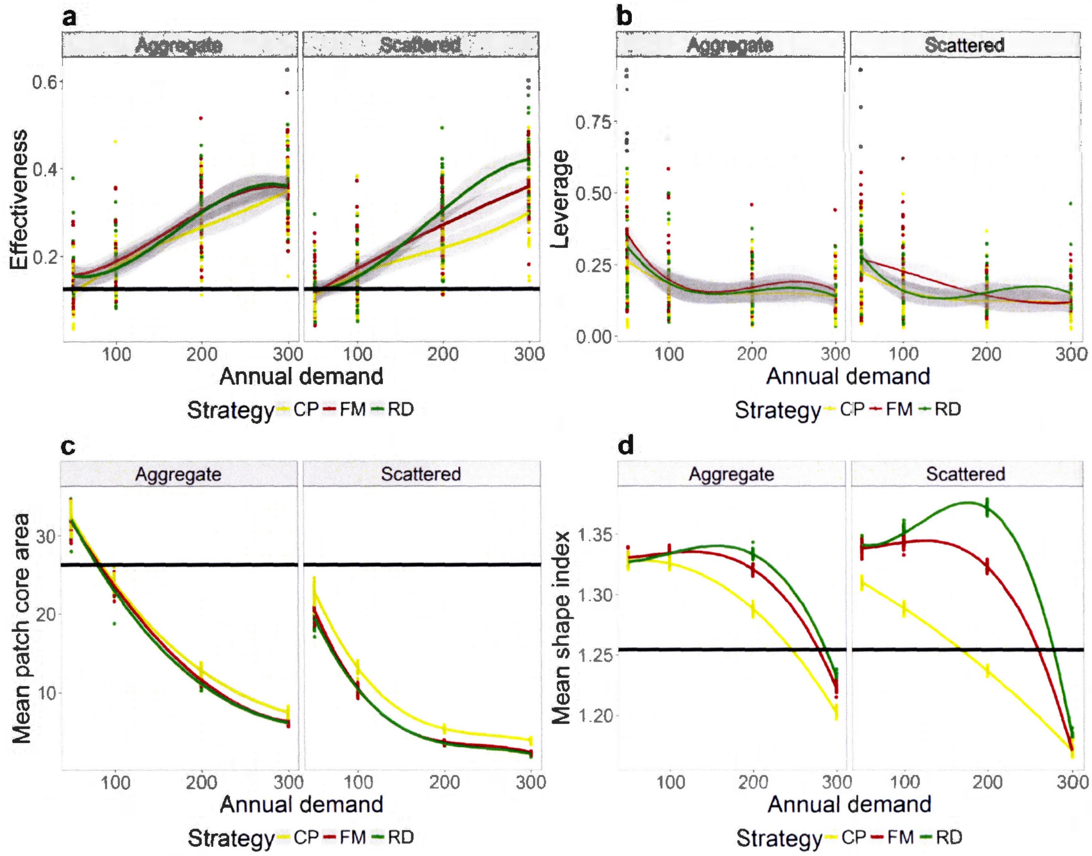

Figure 2.4: Relationship between (a) effectiveness, (b) leverage, (c) forest patches mean core area, and (d) forest patches mean shape index at different agricultural demands (50, 100, 200, and 300 $km^2 \cdot year^{-1}$ are D2, D, 2D, and 3D respectively), according to the strategy (Forest Management, FM; Rural Development, RD; and Crop Productivity, CP) and the spatial pattern of new agricultural patches (aggregate vs. scattered). Response variables are measured over the last 20 years of the simulated period. Solid black line in panel (a) indicates effectiveness of the control scenario with only urbanization, while in panels (c) and (d) it indicates the metric value of the reference year 2010.

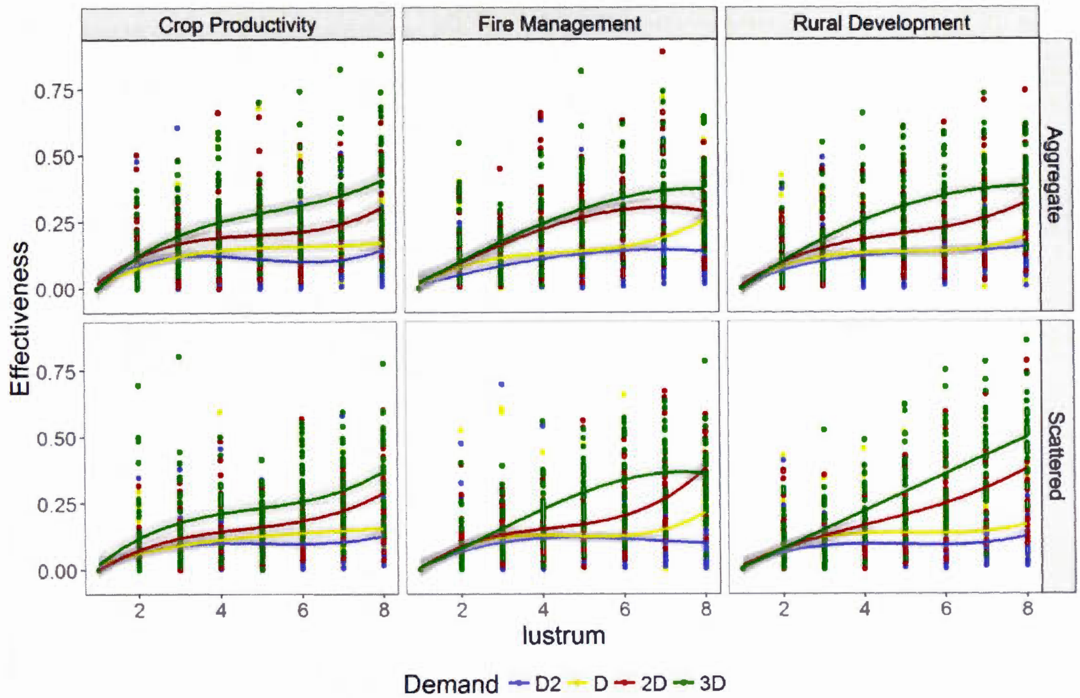

Figure 2.5: Cumulative effect of agricultural conversion on fire suppression effectiveness for each of the 24 landscape scenarios (3 strategies, 2 types of aggregation, and 4 levels of demand) from 2016 to 2050 inclusively.

Table 2.2: Number of years required for a statistically significant improvement on fire suppression effectiveness for each scenario with respect to the effectiveness of the 2016-2020 period. Average number of years for improvement of the scenarios at the same demand level (μ_6), of the scenarios at low vs. high demands (μ_{12}), and of all the scenarios (μ_{24}). Blank value means there were no statistically significant improvement over all the period. Acronyms D2, D, 2D, and 3D stand for the level of agriculture conversion demand in scenarios: 50, 100, 200, and 300 $km^2 \cdot year^{-1}$, respectively.

Strategy:	Crop Productivity		Fire Management		Rural Development		μ_6	μ_{12}	μ_{24}
Pattern:	Aggregate	Scattered	Aggregate	Scattered	Aggregate	Scattered			
Demand: D2		25	15	25	10		19	21	15
D	20	25	25	25	15	25	23		
2D	25	5	10	5	10	15	12	10	
3D	5	15	10	5	5	10	8		

When analysing the performance of scenarios during the last half of the simulated period (20 years), we only found significant differences for a few scenarios (Figure 2.4). When agricultural land was allocated following an aggregated pattern, under all strategies (FM, RD, and CP), the new configurations equally contributed to empowering fire suppression effectiveness (Table 2.3). The three strategies were equally cost-effective in reducing fires (Tables 2.3 and 2.4). On the other hand, when the allocation pattern was scattered, the number of patches and where these patches were allocated significantly modified fire suppression effectiveness (Tables 2.5 and 2.6). Using this allocation pattern, at high demand (2D and 3D) the effectiveness steadily increased when patches were allocated in rural areas, whereas the effectiveness decreased when patches were allocated close to current agricultural land (Figure 2.4a).

At the lowest agricultural conversion rate (D2), fire suppression effectiveness was in any case higher than in the control scenario (that without any agricultural transition; Table E.1). At demand D the mean effectiveness (over the 40-year period) was close to the base-line effectiveness (Table E.2). Even in the last 20 years, when LULC changes had accumulated, effectiveness remained almost unchanged for all D2 and D scenarios (Figure 2.4a). Thus, agricultural demand had to be large enough (at least 2D) to have a notable effect on the fire regime, that is twice the effectiveness of the control scenario. However, when demand was greater (3D) fire suppression effectiveness reached a saturation point for many of the scenarios. This tendency was valid for all the strategies under the aggregate pattern (Tables 2.3 and 2.4). But, when applying a scattered pattern, it was only true for the RD strategy (Table 2.4) while the other two strategies (FM and CP) showed a sustained increase in effectiveness.

The leverage variable mirrored the tendencies observed for fire suppression effectiveness (Figure 2.4b). This cost-benefit ratio behaved similarly for all the scenarios at the aggregate pattern (in accordance with effectiveness behaviour, Tables 2.3 and 2.4). Leverage was reduced by half from D2 to D, whereas it did not experienced change for higher demands. This means that the pressure exerted on the territory by an increasing in agricultural land from D2 to D over the 40 years did not report a clear benefit on fire suppression efforts. For demands over D, LULC changes indicated linear benefits, that is the amount of land changed directly correlated to the area suppressed (Figure 2.5b). Finally, the percentage of large fires ($\geq$ 500 ha) only slightly decreased as natural lands were converted to agricultural use, although this reduction was significant when compared with the control scenario (results not shown).

Under all scenarios, the mean core area of forest patches decreased as agricultural demand increased (Figure 2.4c). However, when agricultural land was aggregately allocated, forest core areas were better preserved (Figure 2.4c). In this case, at the lowest demand level (D2), forests could even gain core area with respect to the initial configuration. Forest patches of different biogeographical regions were unevenly affected by agricultural conversion (Figures 2.6 and E.1). In central and southern coastal regions forest patches lost core area for any level of demand, while in mountainous regions forest accumulated more core area even at D and 2D demands (Figures 2.6 and E.1). That was because the expansion of agricultural land into forests, scrublands, and grasslands was compensated by both afforestation and fire suppression. Overall, the shape of forest patches became more irregular (mean shape index increases), but because of the loss of area, these forest patches also became less complex at the highest demand (Figure 2.4d).

Table 2.3: Analysis-of-variance (type II tests) of the interaction between the quantitative variable (quantity of agriculture conversion, i.e. *demand*) and the categorical variable (*strategy*) on effectiveness of the scenarios when using an aggregate pattern.

	Sum Sq	**Df**	***F* value**	**Pr (>*F*)**
Demand	2.54607	1	475.6755	< 2e-16
Strategy	0.03905	2	3.648	0.02707
demand:strategy	0.00396	2	0.3699	0.69107
Residuals	1.82522	341		

Table 2.4: Coefficients and significance of the linear model $effectiveness|_{\text{aggregate\_pattern}} = f\,(demand, strategy)$.

	Estimate	**Std. Error**	***t* value**	**Pr (>|*t*|)**
(Intercept)	8.28e-02	9.86e-03	8.397	1.22e-15
Demand	8.84e-04	4.05e-05	21.85	< 2e-16
FM	2.49e-02	9.72e-03	2.563	0.0108
RD	2.03e-02	9.72e-03	2.093	0.037

Table 2.5: Analysis-of-variance (type II tests) of the interaction between the quantitative variable (*demand*) and the categorical variable (*strategy*) on effectiveness of the different strategies when using a scattered pattern.

	Sum Sq	**Df**	***F* value**	**Pr (>*F*)**
Demand	3.2647	1	630.303	< 2e-16
Strategy	0.1672	2	16.143	2.00e-07
demand:strategy	0.1591	2	15.362	4.09e-07
Residuals	1.7662	341		

Table 2.6: Coefficients and significance of the linear model $\mathit{effectiveness}|_{\text{scattered\_pattern}} = f(\mathit{demand}, \mathit{strategy})$.

	Estimate	**Std. Error**	***t* value**	**Pr (>|*t*|)**
(Intercept)	3.46e-02	1.01e-02	3.426	6.87e-04
Demand	1.00e-03	4.15e-05	24.116	< 2e-16
FM	3.73e-02	9.97e-03	3.745	2.11e-04
RD	5.33e-02	9.97e-03	5.351	1.60e-07

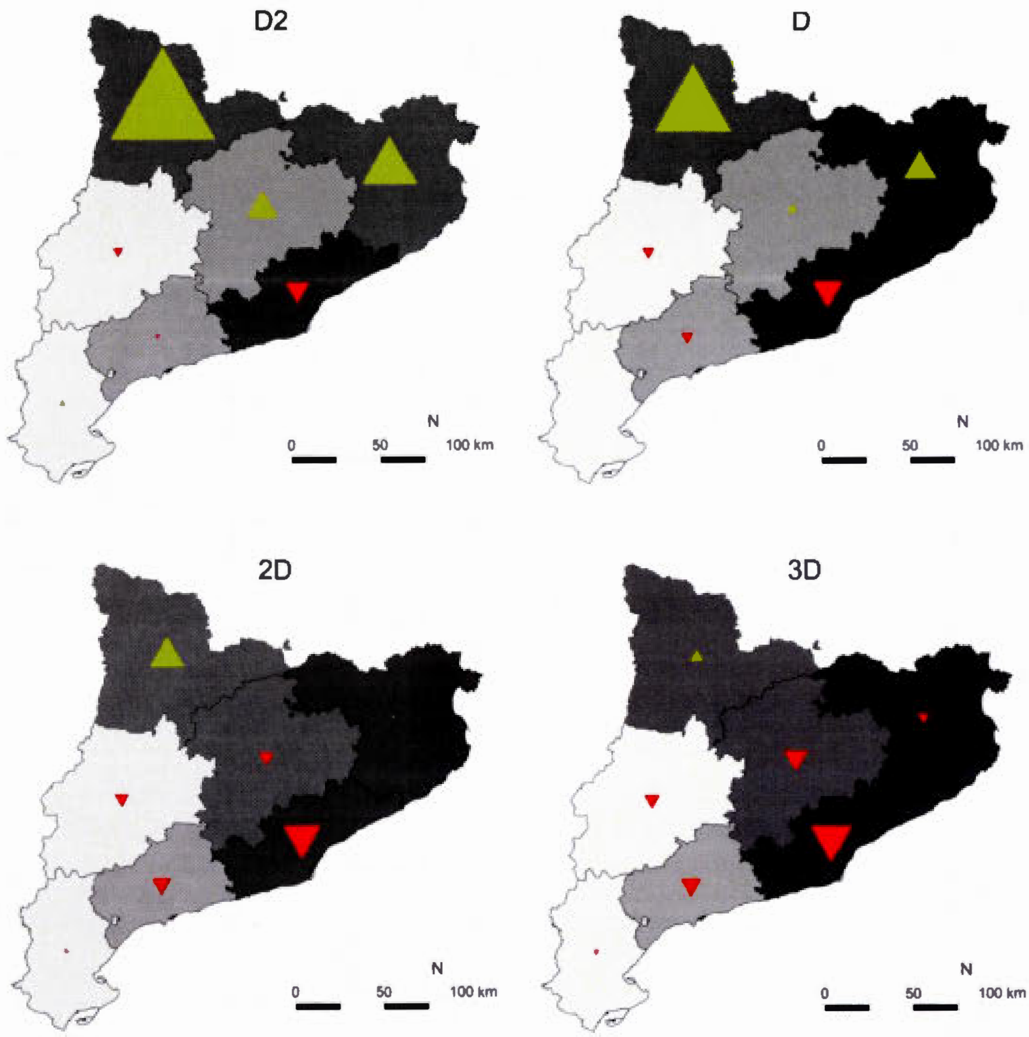

Figure 2.6: Proportional increase (triangles that point upwards) or decrease (triangles that point downwards) of the forest patches mean core area in the 7 *vegueries* (administrative - biogeographic division of Catalonia) as agricultural demand increases from D2 = 50, D = 100, 2D = 200, to 3D = 300 $km^2 \cdot year^{-1}$ (for the Rural Development strategy and the aggregate pattern of allocation). Grey background accounts for the standard deviation of the metric (that increase as grey become darker).

2.5 Discussion

Conversion of natural and semi-natural land covers to agricultural land appears as a potential management alternative for reducing forest fire impacts on fire-prone, highly humanized landscapes (Moreira & Pe'er, 2018). Using a meta-modelling approach combining fire-succession and LULC changes, we were able to assess how land-cover changes induced non-linear responses on the fire regime of a Mediterranean region. Analyzing the fire regime over the last 20 years (once the landscape had already undergone a substantial amount of transformation), both of our hypotheses were partially supported (Figures 2.1 and 2.4a). When changes were aggregately allocated, fire suppression effectiveness remained almost unchanged at low demands, and current fire suppression levels were double only at higher demands (Figure 2.4a and Table E.1). This behaviour confirms in part our first hypothesis, that agricultural conversion has to be considerable to really contribute to an improvement in fire suppression capacity (Figure 2.1a). However, further demand increases did not perform so efficiently: fire suppression effectiveness saturated. The capacity of the landscape to influence the fire regime reached a saturation threshold (Figure 2.1b). Even for relatively fire-resistant landscapes, or for conditions with low fuel loaded landscapes, under favourable weather conditions fires can still impact and spread across the territory (Loehle, 2004). We also detected a time lag between the implementation of the landscape management treatments and a significant increase in fire extinction capacity (Table 2.2). But the delay in empowering the fire extinction capacity decreased as the rate of agricultural land conversion increased (Table D.3). This delayed effect confirms a positive feedback between the amount of new agricultural land and the fire extension capacity. Forest landscapes are complex systems that tend to gradually absorb changes, as long as these are not sharp and sudden (Reyer *et al.*, 2015). It is frequent to observe a time lag or resistance to changes before any significant reaction occur (Scheffer *et al.*, 2001).

When croplands were aggregately allocated the fire regime similarly responded (Figure 2.4a). We could ascribe this behaviour to the fact that the natural land available to accommodate new large agricultural patches was scarce, and became even scarcer over time (Figures E.2, E.3 and E.4). Close to the end of the period, the allocation prioritization of any strategy became similar (Figures E.3 and E.4). Thus, when patches were forced to be large, the landscape itself had a smaller or limited capacity for these patches to extend. The transition-potential map lost its predictable power and the spatial distribution of new patches tended to converge across strategies. But when agricultural land was sparsely allocated, both strategies that break forest continuity contributed to a larger extent to reducing fire impacts (Figure 2.4a). Therefore, smaller agricultural patches have to be thoughtfully allocated to strengthen fire extinction capacity.

At equal demand, treatments using an aggregate pattern reported on average a higher leverage (Figure 2.5b, Table E.2). The scattered pattern required more LULC change efforts to create potential fire breaks on the landscape. Moreover, in landscapes where croplands were aggregately allocated, forest core areas were better preserved, so avoiding negative edge-effects (Brudvig *et al.*, 2012). Despite the applied transformation to agricultural lands, at intermediate demands (D), mean forest core area increased in the northern part of the study area, from west to east (Figures 2.6 and E.1). Northern sub-regions contain most of the mature forest cover in Catalonia (Figure C.1). Thus, agricultural conversion could be compensated by increased fire suppression (that eliminates potential regeneration failures, i.e. forests becoming scrublands) and by afforestation (colonization of scrublands by woody plants). However, in south-central sub-regions, forest cover is already quite fragmented and cannot bear further pressure added by agricultural conversion. In addition, afforestation in the south is slower than in the north because of higher fire recurrence and less favourable conditions (climate is drier and warmer) for forest species to establish in already stable scrublands communities (Lloret *et al.*, 2005).

2.5.1 A meta-model for fire-prone landscapes integrating natural and anthropogenic drivers of change

Our meta-model has proven to be a useful spatially-explicit tool to explore feedback interactions between natural and anthropogenic drivers of global change often neglected in most landscape-scale studies (Hantson *et al.*, 2015). Modelling highly humanized fire-prone landscape dynamics from a coupled human-natural systems perspective mainly means to incorporate LULC changes, fire behaviour, fire suppression efforts, landscape management, and forest ecological processes. To our knowledge, our work is the first attempt to model for an entire fire-prone region the interplay between land-cover transitions, fire suppression, and fire behaviour in a landscape management context. At the local level, Loepfe *et al.,* (2012) also used a modelling approach to evaluate agriculture conversion, close to and far away from croplands, as a fire smart management strategy. They combined this fuel-reduction strategy with an increase in fire suppression effectiveness and a reduction in ignition frequency with respect to the empirical base-line. They showed that the integration of long-term landscape planning efforts could help mitigate climatic effects on future fire regimes more than traditional fire extinction plans.

This modelling framework allows us to explore the cumulative effects of landscape changes over time. A possible next important question may be: Until when these spatial legacies allow fire suppression efforts to benefit from opened landscapes? However, to study long-term cumulative effects and create plausible results, landscape-scale models should explicitly include the impacts of climate change on ecological processes and disturbance regimes (Keane *et al.*, 2015). Variations in temperature and precipitation would influence vegetation dynamics at the stand level, potentially altering biomass accumulation, post-fire regeneration, colonization of scrublands by woody species, and drought-induced mortality. Modelling vegetation dynamics in response to predicted climatic change has been addressed using multiple modelling approaches (from empirical-based to process-based), over a wide range of ecological scales (individuals, populations, functional types, mono-dominant forests), and areas (from stands to biomes) (Peng, 2000; Mouillot *et al.*, 2002; Seidl *et al.*, 2012). Though, all or some disturbance regimes, forest management activities, and LULC changes are missing in many of these studies (Keane *et al.*, 2015; Rammer & Seidl, 2015). We plan to improve the MEDFIRE model by making productivity, recruitment, colonization, and mortality climate dependent. Once coupled to the MEDLUC model, we will then be able to explore longer timelines of such fire-prone coupled human-natural systems.

2.5.2 Implications for managing fire-prone landscapes in view of global change

Global change poses new challenges for researchers and governmental institutions interested in managing forests in a sustainable and resilient manner (Messier *et al.*, 2015). Despite the widely accepted claim that climate change will increase vulnerability of fire-prone landscapes to more intense and recurrent wildfires, there is still room for improving to better cope with future conditions. Here, we have proposed alternative landscape-scale management options for reducing system exposure to a frequent severe natural disturbance and positively fostering ecosystem resilience in view of rigorous environmental pressures associated with global change (Chapin *et al.*, 2010). We advocate, that in weather-driven fire regimes (sensu Pausas

& Fernández-Muñoz, (2012)), creating discontinuities on unstructured fire-prone landscapes will lead to significant gains in fire-fighting capacity. Through changes in the spatial distribution of forest cover, agricultural conversion seeks to prevent fires from burning out of control, and ultimately to diminish fire recurrence. It is already a first step in supporting ecosystem resilience in Mediterranean-type regions where large fires account for most of the burnt area and high recurrence and intensity endanger functionally rich ecological regeneration (Archibald *et al.*, 2009). Hence, the opened gaps in irregular forests offer extinction opportunities to fire brigades by facilitating the access to the fire perimeter, reducing overall fuel-load and eventually fire intensity, and creating fire-breaks that contribute to slowing down or even stopping the advancing front (Loepfe *et al.*, 2010). These strategies do not eliminate fire events from the system. Such a goal is economically unfeasible and ecologically undesirable (Donovan & Brown, 2005; Moritz *et al.*, 2014). Actually, successful fire exclusion in fire-prone regions has triggered unprecedented fuel build-up and homogenized landscapes over decades (Keeley, 1999; Keane *et al.*, 2002), creating the baseline conditions to overwhelm whatever fire suppression efforts are put in place when multiple major fires impact on a region.

There is still an open debate about whether and how fuel management can mitigate fire risk under new global conditions. There is strong evidence showing that fuel management by itself cannot contribute to the reduction of neither fire incidents nor carbon emissions (Campbell *et al.*, 2012; Price *et al.*, 2015); although some modelling exercises have concluded that such approaches may control final burnt areas (Stephens *et al.*, 2009; Khabarov *et al.*, 2014). However, it is unlikely that sylvicultural interventions such as thinning or wood chipping and prescribed burnings can reasonably modify fuel loads and forest continuity to the point of altering high intensity fires because (1) at least 30% of the landscape has to be treated, which implies unacceptable economic costs unless economic profitability of this wood is ensured, (2) random allocation of treatments greatly reduces efficiency, so a careful search of optimal locations is need, and (3) inadequate spatial aggregation of fuel treatments reduces the efficiency of the interventions (Finney, 2001; Loehle, 2004). When planning a fuel management intervention is important to identify the location of treatments and, to a lesser extent, their intensity (Ager *et al.*, 2010). Only a few authors have used scenario exercises to investigate the role and location of fire management intervention areas on the fire regime (Parisien *et al.*, 2007; Regos *et al.*, 2016). In the present study, we explicitly focused on finding out whether the location of the treatment (through the transition-potential map linked to each strategy; Figure 2.3) and the spatial pattern (aggregate vs. sparse; Figure D.2) could influence the fire regime. Our results suggest that allocating crops in an aggregate pattern offers slightly more opportunities to suppress fires. But if socio-economic or environmental constraints restrict the allocation to smaller and sparse patches, then the spatial distribution needs to be carefully outlined and implemented. In such cases, it becomes crucial to collaborate with fire behaviour experts to identify strategic locations across the territory for fire pre-suppression activities. A strategic location for fuel management is defined as (1) an area with a specific forest structure that if appropriately managed can modify the behaviour of a future fire and prevent it from shifting to an uncontrollable wildfire, and (2) a geographic position accessible to the fire-fighting crews that is also likely to receive a burning front (Syphard *et al.*, 2011). Thus, the combination of stakeholders knowledge and robust modelling tools integrating multiple natural and anthropogenic drivers of change becomes a win-win option to handle resilience-based forest management of fire-prone landscapes.

Further studies should investigate the economic viability and social acceptance of such alternative fire-reduction treatments, as well as a detailed environmental impact to complete the data portfolio needed to fully inform a decision-making process. A careful economic and ecological monitoring of trade-offs over time is indeed advised.

It is highly likely that socio-political issues could arise if such treatments are to be implemented in a European Mediterranean region. Even if both the scientific community and stakeholders agree that current fire suppression policies are behind large devastating wildfires, society is not ready for rethinking fire prevention nor fuel-reduction management strategies yet (Calkin *et al.*, 2015). Letting natural fires burn under strict control (as long as meteorological conditions are not extreme) is another sound option to reduce fire risk at the landscape level (Regos *et al.*, 2014), and is already being applied in remote areas of Canada. Though, the inclusion of managed wildfires in forest plans across the United States has had little acceptance among the general public (North *et al.*, 2015). Likely, agriculture conversion will find many detractors. But, unless we start to value the long-term ecological benefits and cost savings of alternative landscape management strategies over classic fire suppression, fire-prone regions will continue to be at risk of losing adaptation opportunities to cope with a changing future.

2.6 Acknowledgments

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CHAPTER III

ENHANCING FOREST RESILIENCE TO GLOBAL CHANGE: MANAGING TREE FUNCTIONAL DIVERSITY AND CONNECTIVITY IN FRAGMENTED LANDSCAPES

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3.1 Abstract

Forest functioning is currently being challenged by interacting drivers of global change. Cutting-edge forest management approaches advocate fostering forest ecosystem resilience. To support resilience-based forest management, new tools and methods to quantitatively describe forest resilience are needed. Here, we present a multi-dimensional evaluation of ecological resilience based on (1) species functional response traits and (2) forest network properties (e.g. connectivity, modularity, and centrality). Using a fragmented rural landscape in temperate south-eastern Canada as a reference landscape, we applied this new approach to compare a set of alternative management scenarios for the purpose of enhancing the resilience of forest patches to disturbances. Two contrasting strategies were implemented: functional enrichment of current forest patches, and an increase of the forested area through plantations. For both strategies the planted species were either biodiversity enhancer, drought tolerant, or pest resistant. We investigated how the reference and the managed landscapes responded to three disturbances: drought, pest outbreak, and timber harvesting. All management actions increased both overall response diversity and connectivity. Indeed, when the less functionally diverse patches were managed first, functional enrichment was much more effective than plantations in increasing ecosystem resilience. Enriching with pest resistant species actually increased resistance to an outbreak more than twice compared to enriching through drought tolerant or biodiversity enhancer species. Biodiversity enhancer species mitigated drought effects equally as well as drought tolerant species. Thus, in fragmented forested landscapes facing unknown environmental conditions and disturbance regime shifts, the best insurance option is maximizing functional diversity of current forest landscapes, thus increasing biodiversity, rather than allocating new polycultures. In addition, forests could cope with harmful pest outbreaks only if tree species resistant to insects and disease predominate.

Keywords: Network topology; Modularity; Centrality; Functional redundancy; Response diversity; Drought; Insect pest; Harvesting; Rural landscape

3.2 Introduction

Forest ecosystems face rising temperatures, recurrent and prolonged periods of drought, extreme climatic events, biotic homogenization, fragmentation and anthropogenic degradation, altered natural disturbance regimes, and in many cases a combination of many of these environmental and anthropogenic pressures with unknown cascading effects on ecosystems functioning and overall biodiversity (Raffa *et al.*, 2008; Lloret *et al.*, 2012; Buma, 2015; Seidl & Rammer, 2016). Fostering biodiversity and functionally rich forest ecosystems is at the base of ecosystem services and goods provisioning, from which humans depend on (Gamfeldt *et al.*, 2008). Global change and the inherent uncertainty thus pose novel challenges in managing forests in a sustainable way. Yet, former and current management approaches do not often consider the need for adaptation of forest ecosystems to future environmental conditions (Gustafson, 2013). Different cutting-edge forest management approaches have been proposed, but thus far, the most promising option is to manage for forest resilience to ensure the provision of services and the adaptation of forest ecosystems to unknown future conditions (Messier *et al.*, 2013). Resilience is here understood as the capacity of the ecosystem to absorb environmental changes (pressures) and cope with natural and anthropic disturbances (pulses) without losing its main functionality, while get better prepared to face future disrupting exogenous conditions (Holling, 1996; Gunderson, 2000). However, measuring and monitoring resilience, and ultimately managing for it in complex ecological systems such as forest landscapes, has proven to be challenging (Newton & Cantarello, 2015; Timpane-Padgham *et al.*, 2017).

Different approaches have been proposed to operationalise resilience management of natural ecosystems (Folke *et al.*, 2002; Anthony *et al.*, 2015). In forest ecosystems, identifying the range of natural variability in an ecosystem determines the basins of attraction of the system which in turn allows one to measure recovery trajectories as a means of characterising resilience to natural disturbances (Seidl *et al.*, 2016). Other approaches are based on key resilience indicators such as resistance to disturbance, time of recovery after a perturbation, and variability (Palumbi *et al.*, 2008; Côté & Darling, 2010; Carpenter *et al.*, 2011; Cole *et al.*, 2014). However, as forest landscapes are intrinsically spatial entities, these approaches to quantify resilience do not take into consideration that disturbances and changing environmental conditions will come up against the spatial organisation of forest patches in terms of their composition, age, size, and isolation (Turner *et al.*, 2013). When considering forested landscapes as a set of individual forest patches (stands) within a matrix of altered natural and human-build elements, one can take a network approach to determine the resilience of such ecosystems (Gonzalès & Parrott, 2012). As such, Webb & Bodin (2008) enumerated five interdependent conditions that potentially can ensure the resilience (or robustness (Levin & Lubchenco, 2008)) of a network: (1) diversity of the components, (2) redundancy of these components, (3) modular structure, (4) control of flows within the system by central elements, and (5) connectivity between the components. Modular systems (or networks) are structured in modules or groups of highly interconnected elements (nodes) that are loosely connected to elements (nodes) of other modules (Solé *et al.*, 2003). Central entities are those network nodes that concentrate most of the connections (hubs) and/or bridge two sub-sets of nodes that otherwise will be disconnected (connectors) (Estrada & Bodin, 2008). We acknowledge that these five conditions characterize the resilience of a forest landscape, but we recognize that ecosystem resilience can be better achieved by first targeting species with response traits specific to disturbances and changing conditions of the environment (Suding *et al.*, 2008; Mori *et al.*, 2013). Thus, to be resilient a forest landscape should have the following five complementary resilience related properties: functional redundancy, response diversity, landscape connectivity, modularity, and centrality.

By conserving functionally different species, ecosystem structure and functions are likely guaranteed and resilience maintained (Díaz & Cabido, 2001; Cadotte *et al.*, 2011). Response diversity contributes to ecosystem stability when natural disturbances, environmental changes, or anthropogenic pressures enable different species to partition an available niche (Elmqvist *et al.*, 2003; Mori *et al.*, 2013). Yet, functional redundancy is also an important property that ensures that other species will be able to play the same role following natural and anthropogenic disturbances (Pillar *et al.*, 2013). Redundancy has to be measured in a multi-dimensional functional space (Rosenfeld, 2002), and over the whole environmental gradient so as not to underestimate superfluous species that could become the main, even the essential, functional contributors (Wellnitz & Poff, 2001). As functionally equivalent species may not respond similarly to changing environmental conditions, it is imperative to differentiate effect traits (e.g. nutrient cycling or soil retention) from response traits (Naeem & Wright, 2003; Suding *et al.*, 2008).

To resist and/or recover from rapid climate change and compounded natural disturbances, forest ecosystems may benefit from high connectivity between patches (favouring exchanges of functionally distinct species, and genes) to foster adaptability to new environmental conditions. Indeed, after disturbances that can potentially remove entire forest patches, landscape connectivity of the biological remnants will be essential for forest landscape recovery (Franklin *et al.*, 2000; Lindborg & Eriksson, 2004). On the other hand, although structured connectivity fosters ecosystem resilience, it can also have deleterious effects on the landscape when faced with a disturbance that can spread. For example, a highly connected forest landscape along with the right environmental conditions could contribute to a growing spatial distribution of a disease (e.g. the sudden oak death outbreak in Western US (Ellis *et* *al.*, 2010)). Similarly, continuous forest patches with a dense understory are more vulnerable to unexpected large wildfires than rural landscape mosaics or landscapes with strategic fuel breaks (Archibald *et al.*, 2009; Syphard *et al.*, 2011; Pausas & Fernández-Muñoz, 2012). Modularity or compartmentalisation has proven to be an effective defensive strategy against fire or pest and pathogen outbreaks because modules have the capacity of buffering the spreading of disturbance and thus avoiding ecosystem collapse (Stouffer & Bascompte, 2011). In a forest landscape, if modules (i.e. groups of highly connected similar forest patches) are completely disconnected or the dispersal potential of the perturbation is lower than the separation between these modules, then the capacity to limit the spread of the disturbance is high, but it will decline with modularity (Christley, 2005). Finally, centrality refers to the multiple ways an element can influence the flow of energy, nutrients, organisms, or genes across a landscape (Borgatti, 2005; Iyer *et al.*, 2013). In a forest landscape network, central patches are those that: (1) contribute the most to the traversability of the landscape, that is the reachability of all nodes from any node, (2) act as a bridge between modules and often connect isolated nodes, (3) have higher recruitment potential (of functionally distinct species and variety of genes) because of their disproportional area, or (4) have a high proportion of the shortest paths between pairs of nodes within the network going through them, and thus form the backbone of the network (Urban & Keitt, 2001; Bodin & Norberg, 2007). Central patches in a forest landscape will therefore be responsible to gather, and disperse from, a large proportion of the species and functional diversity of the landscape. Identifying the central patches and their connexions also helps in the design of more effective pest-mitigation plans. Indeed, low centrality may weaken the response capacity of a landscape facing harmful attacks (Janssen *et al.*, 2006).

Here, we introduce a multi-dimensional evaluation of resilience that links tree species functional response traits (the selected traits describe how species respond to changing environmental conditions, climate and disturbances) and the topology of the forest patches network. We provide precise measures for the two tree-level properties (functional redundancy and response diversity) and the three landscape-level properties (connectivity, modularity, and centrality) to quantify forest ecosystem resilience to disturbances. We show the applicability of the functional trait-network approach to assess the level of resilience of a rural landscape of mixed forest and agriculture patches in temperate south-eastern Canada where a long history of agricultural pressure and commercial harvesting of only a few species have resulted in a fragmented and homogenised forest cover. We then use a simulation approach to explore ways to improve landscape resilience by either functionally enriching current forest patches or increasing forest area with new multi-species plantations. Lastly, we examine how the reference and the simulated landscapes might respond to three disturbances that currently (or will in the future) impact temperate forests across eastern North America: timber harvesting, pest outbreaks, and drought (Boulanger & Arseneault, 2004; Hogg & Bernier, 2005; Cyr *et al.*, 2009; Bonsal *et al.*, 2011). We adopt a static modelling approach to analyse the behaviour of the five resilience-related properties of the initial, managed, and disturbed landscapes. We therefore do not account for the dynamic nature of the forest communities, nor the regeneration and establishment processes happening after any disturbance.

We expect that overall resilience of this rural landscape will be relatively poor due to the low functional diversity of forest communities and the unstructured topology of the underlying network of forest patches (that is, a non-modular network with little key nodes that centralize and boost ecological flows). We foresee that by managing this landscape with the proposed strategies (1) functional response diversity will increase under both management strategies, (2) but as a trade-off, functional redundancy will decrease, and (3) functional connectivity will improve, particularly in landscapes with new forest plantations. In addition, we hypothesise that (1) natural disturbances rather than harvesting will mostly reduce functional response diversity (in both, the reference and the simulated landscapes), (2) pest outbreaks will be the most harmful disturbance because of the high specificity of this disturbance, and (3) harvesting will greatly alter network topology, reducing the connectivity of any network and likely removing important central nodes.

This functional trait-network analysis approach will allow us to compare the resilience of the different simulated landscapes and the effects of various disturbances on these landscapes, and then propose efficient interventions to maximise resilience to global change factors.

3.3 Materials and methods

3.3.1 Study area and sampling design

The Central Quebec region (south-eastern Canada, 45°35' N - 46°34' N, 72°59' - 71°22' W) is a rural mosaic of forest and agricultural patches ca. 7 000 km^2 (40% is forest covert) in the temperate biome (Figure 3.1). We inventoried 42 sites across the landscape (hereafter the reference landscape) covering a wide range of ages, dominant forest types, and agriculture predominance (average area was 8.71 ± 1.25 ha, mean ± SE). Within each site, we sampled 8 to 14 circular 0.02 ha plots (1 586 in total), spaced 50 m and 10 m away from the edges of forest patches (Craven *et al.*, 2016). All trees with diameter at breast height > 10 cm were included, and 34 tree species were identified (Table F.1). Tree communities were characterized by species abundance (# trees · ha^{-1}), and sites were then classified as either deciduous forest (>

75% deciduous species) or mixed forest (25 - 75% deciduous) according to the eco-forest maps of the region (MFFP, 2006). This binary classification allowed us to broadly characterize these two types of forest to be used later on the characterization of all forest patches in the region. On deciduous sites 32 species were found, whereas on mixed sites 27 species were found. To assess the functional diversity of tree communities, we selected eight functional traits that contribute to species capacity to respond to both multiple disturbances and environmental changes. We focused on available response traits for the 34 species of the Central Quebec region, those directly related to disturbance coping such as drought, shade, and water-logging tolerance, and those related to resistance to and regeneration after disturbance such as maximum tree height, wood density, mode of reproduction, seed mass, and seed dispersal vector (Table F.2). Functional trait values were obtained from the TOPIC database (Aubin *et al.*, 2012) and from the literature (Niinemets & Valladares, 2006; Miles & Smith, 2009), while species maximal seed dispersal distance was estimated following Tamme *et al.*, (2014) (Craven *et al.*, 2016) (Table F.2).

3.3.2 Functional network

We sought to represent the fragmented rural landscape of Central Quebec as a network of forest patches. In this framework, nodes of a network represent forest patches, and each node accounts for the estimated intra-patch functional diversity of its tree community. Network links exist between patches that are close enough for species to be able to disperse seeds, and account for the proportion of intra-patch functional diversity between nodes (according to species dispersal capacity). The resulting so-called functional network describes the spatial distribution and topology of tree communities, but also accounts for the whole functional diversity of the forest landscape and the likelihood this functional diversity can disperse across the network, that is, the overall functional connectivity of the landscape.

Based on a map of the study area (MFFP, 2006) accounting for forest and non-forest cover at a 1 ha · pixel^{-1} resolution we first identified the forest patches (based on an eight-neighbour rule) and then calculated the minimum Euclidean distance between patches (calculated from their perimeter) using the SELES software (Fall & Fall, 2001). Nodes of the network were defined as forest fragments larger than 5 ha; this lower limit of patch area constitutes the size of the smallest sampling site. We derived the complete graph representing the fragmented forest landscape, with n = 1060 patches (average area = 264 ± 2706 ha, mean ± SE), with in-degree and out-degree of all nodes equal n-1, and links accounting for the minimum Euclidean distance between patches (Figures 3.1 and 3.2).

We then estimated species richness, composition and abundance within each node. First, to estimate species richness, we built a species-area relationship for each forest type (mixed and deciduous) using the 42 surveyed sites and extrapolation methods implemented in the *iNEXT* R-package (Chao *et al.*, 2014) (Figure 3.3). We treated mixed and deciduous forest cover separately as previous analyses revealed differences in functional and species diversity between these forest types (Craven *et al.*, 2013). We completed 1000 random selections with replacement of groups of s = 1 to 42 sites to fit a linear relationship between the average area (ha) and the size s of the group of sampled sites (it resulted in $y = 0.002 + 0.115 \cdot x$). Within the 1060 patches, we identified the area corresponding to deciduous and mixed forest types (MFFP, 2006). We applied an interpolation by cubic splines of the species diversity curves (Figure 3.3) to estimate the number of species within each forest type area. These estimations were systematically truncated to 32 species in deciduous areas and to 27 species in mixed areas to emulate species richness of the reference landscape (that is, to not estimate beyond the maximum observed diversity at the site scale). Then, we estimated the species composition of each patch by selecting species from the regional pools of 32 deciduous and 27 mixed forest species weighted by species relative abundance per forest type (Figure F.1). Finally, we aggregated the abundances of the coincident species to arrive at the estimated species richness of the network forest patches (Figure F.2).

The functional diversity of tree communities within patches was quantified by the abundance-weighted functional dispersion index (*FDis*). *FDis* accounts for how functionally different the species are from one another in a community (Laliberté & Legendre, 2010), and is mathematically independent of species richness. Following Craven *et al.* (2016), *FDis* index was computed using a generalisation of the Gower's distance (Pavoine *et al.*, 2009), and a lingoes correction was applied to get an Euclidean functional dissimilarity matrix (a species-by-species distance matrix based on the functional response traits of the eight species).

Links between nodes of the network were established based on the distance between forest patches and their species composition. Two nodes of the network separated by a distance d were effectively connected only if at least one tree species could disperse (according to species dispersal capacity) up to that distance d. Because each node has a particular species composition, a link L_{ab} could exist from node a to node b, but not necessarily vice versa. The weight of the directed link L_{ab} was the proportion of functional diversity of the source node that could travel to the target node (i.e. $w_{ab} = FDis_{ab} / FDis_a$ where $FDis_{ab}$ was calculated for the tree sub-community in node a consisting only of species able to disperse to node b). As a result, we then obtained a directed weighted graph (Figure 3.2).

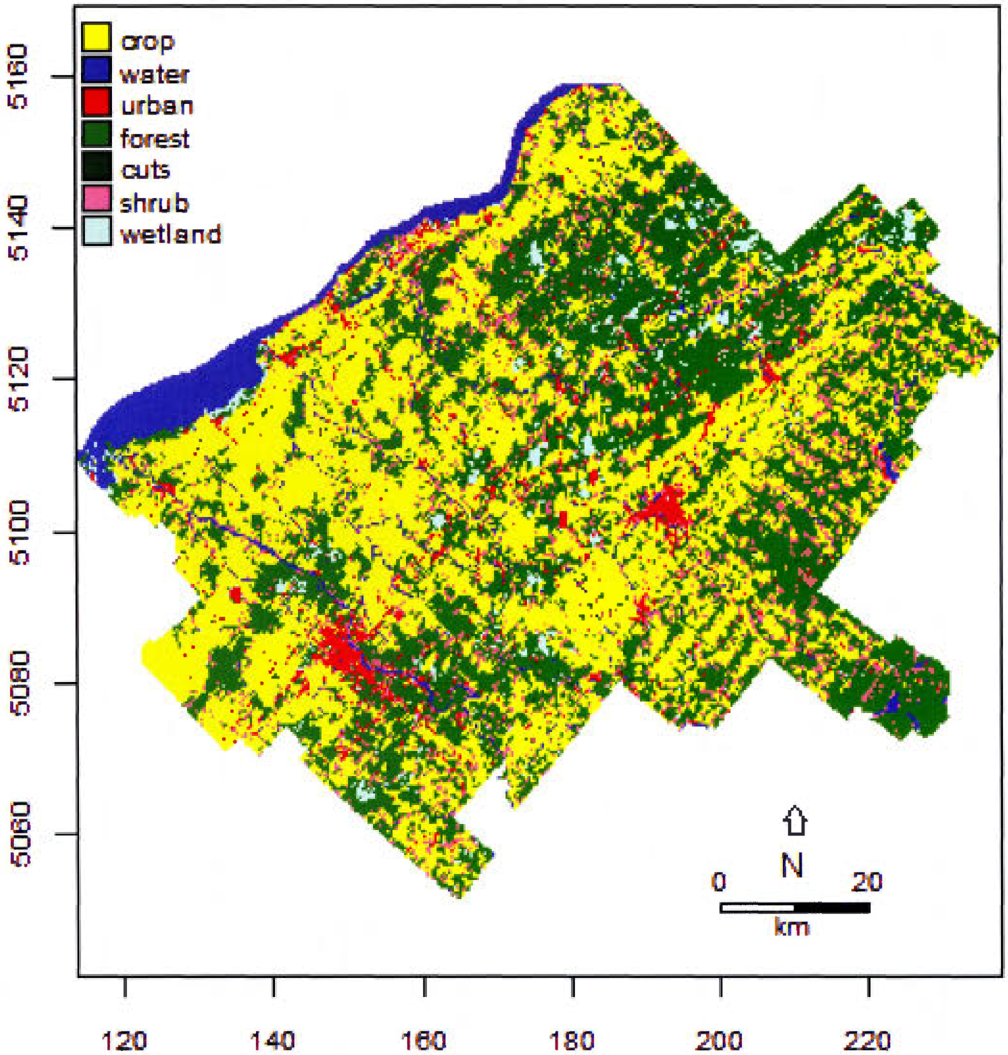

Figure 3.1: Land-cover map of the Central Quebec region with seven landscape elements at 1 ha spatial resolution (units on the *x*-axis and *y*-axis are in km).

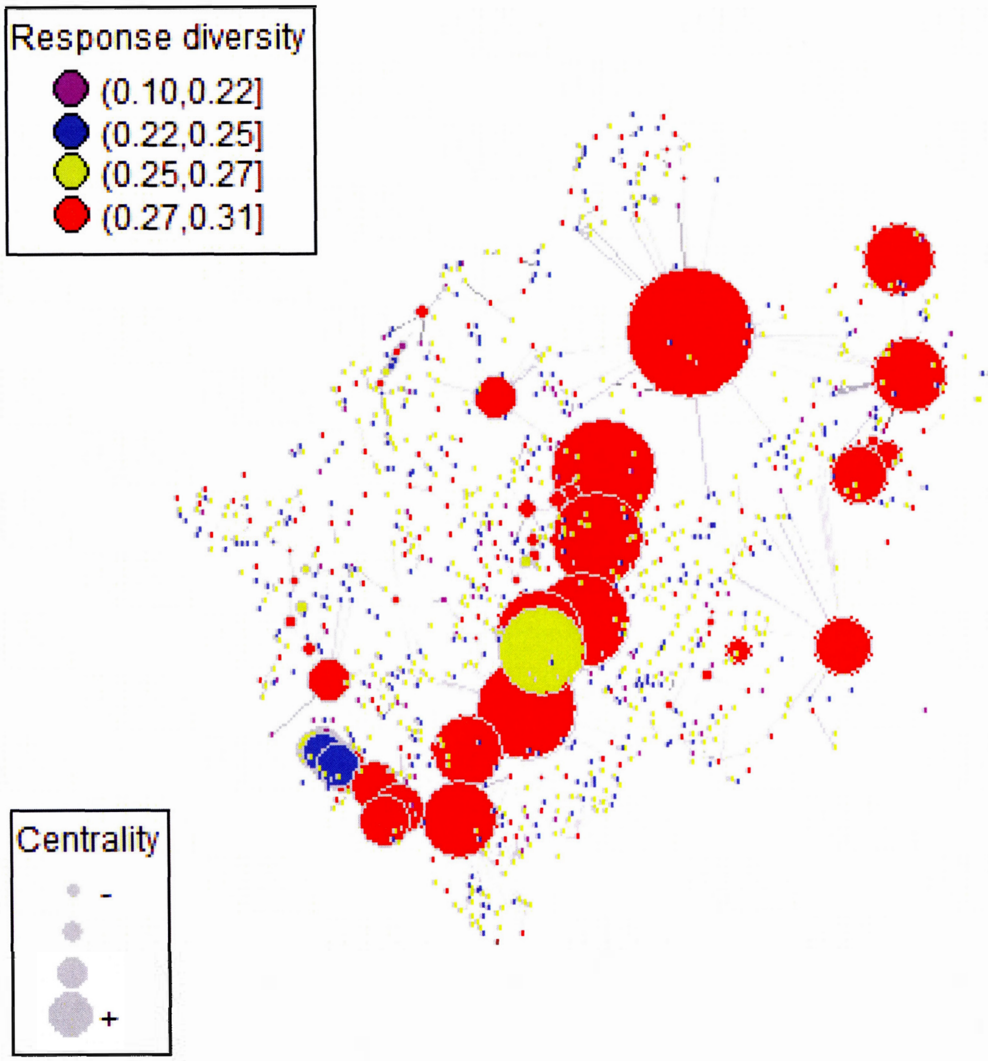

Figure 3.2: Functional network representing the reference landscape. Node's size is proportional to the betweenness centrality index BC^{PC} and node's colour varies along functional diversity index *FDis*. The BC^{PC} index of a node measures the number of shortest paths between each pair of nodes that pass through that target node. Nodes with high BC^{PC} values are those that control most of the network flow and constitute the backbone of the forest network.

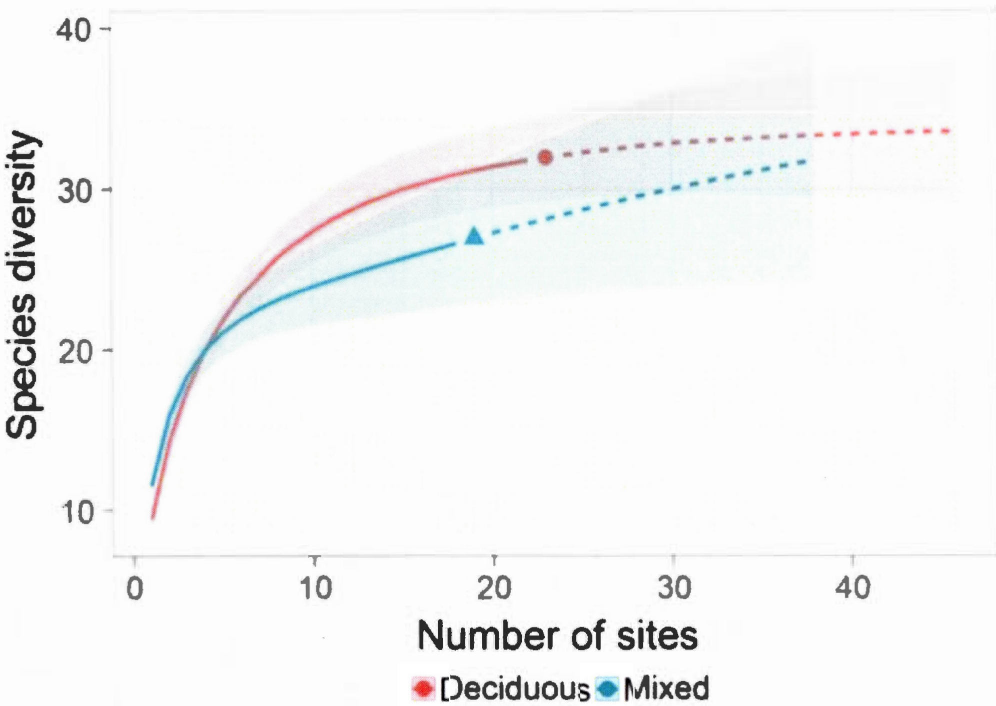

Figure 3.3: Species accumulation curves for deciduous and mixed forest patch types.

3.3.3 Measures for the five resilience related properties

We quantified five properties that are thought to influence resilience: (1) landscape-scale response diversity *RD*, (2) landscape-level functional redundancy *FR*, (3) functional connectivity as the probability of connectivity index *PC*, (4) modularity *Q* of the of the network, and (5) centrality of each patch as the mean of the patch-level generalized betweenness centrality index BC^{PC}.

Response diversity *RD* was measured as the *FDis* diversity index of the whole tree community in the network (Laliberté & Legendre, 2010). Network-level functional redundancy *FR* was calculated as proposed by Ricotta *et al.*, (2016), $FR = 1\text{-}RaoQ/D$ where *RaoQ* is the Rao's quadratic entropy (Equation F.1; that measures the average functional dissimilarity of an individual or community from the whole assemblage) and *D* is the Simpson Index (Equation F.2). Both indexes *RaoQ* and *D* are implemented in the *FD* R-package (Laliberté & Legendre, 2010). The connectivity index *PC* measures the probability that two points in the landscape are reachable within the same forest patch or through connected patches (Equation F.3) (Saura & Pascual-Hortal, 2007). By applying Equation F.1, *PC* accounts for the connectivity of functional diversity across the landscape. Modularity *Q* of the network was calculated by the edge-removal algorithm of Newman and Girvan, (2004) (Equation F.4), where removal prioritization is based on an edge betweenness index. A network with modular structure similar to that of a randomised network, has *Q* close to 0, while *Q* values above 0.3 indicate a significant community structure, whereas values above 0.7 are rare (Newman & Girvan, 2004). The community structure and modularity *Q* were extracted with functions on the *igraph* R-package (Csardi & Nepusz, 2006). The BC^{PC} centrality index captures the relevance of a particular node within the set of all shortest paths in the network (Equation F.5) (Bodin & Saura, 2010). Nodes with relative higher BC^{PC} index constitute the backbone of the network (Bodin & Norberg, 2007). Values of connectivity PC, modularity Q, and functional redundancy FR indexes are in the range [0,1], response diversity RD and centrality BC^{PC} indexes have a default minimum of 0 but do not have an upper limit. We used Conefor software to compute the PC and BC^{PC} indexes as it also handles directed non-complete weighted graphs (Saura & Torné, 2009).

3.3.4 *Simulation of management strategies and forest disturbances*

We simulated two distinct forest management strategies, functional enrichment of current forest patches and increase of forest area by establishing new plantations in non-forested areas. The functional enrichment strategy mainly sought to improve functional response diversity of tree communities, whereas in the plantation-based strategy the main goal was to enhance overall landscape functional connectivity. We first simulated three management intensities (or amounts of target area to be managed), 10 000, 40 000 and 70 000 ha, under both strategies, functional enrichment and plantations. That is, either 10 000 ha of current forest were functionally enriched or 10 000 ha of land were converted to forest polycultures. Both strategies were implemented at a density of 1 000 trees ha^{-1}. We then focused on where to concentrate the managing efforts. In the functional enrichment strategy we differentiated whether enrichment should be done in the most functionally poor nodes (*LessD* in Table 3.1), in loosely connected nodes (*LowC* in Table 3.1), or in highly connected ones (*HighC* in Table 3.1). Poorly connected nodes verified $dPC_k < \text{median}_k(dPC_k)$, and highly connected $dPC_k \geq \text{median}_k(dPC_k)$; where $dPC_k = 100 \cdot (1 - PC_k/PC)$ and PC_k is the same PC index after the removal of node k, and accounts for the node k contribution to overall network connectivity (Saura & Pascual-Hortal, 2007). In any case, we limited the enrichment effort to a maximum of 2 000 ha per forest patch. In the plantation strategy, two spatial distributions for plantations were considered: randomly scattered across the landscape (*Rand* in Table 3.1) or strictly along riparian zones (*Ripa* in Table 3.1) (Figures F.3 and F.4). New forest patches were allocated in agricultural land, scrublands, or recently harvested areas (Figure 3.1), and spatially separated from current forest patches and other plantations by at least 1 ha. Plantation size was uniformly distributed in the ranges 50 ± 10, 200 ± 40, and 350 ± 70 ha respectively for the 10 000, 40 000, and 70 000 ha target area intensities. This resulted in 11 specific management strategies (Table 3.1).

To implement these 11 management strategies, three tree species from the pool of species in the region were selected to either enrich a current patch or be planted in a new patch. Tree species with some key functional traits were prioritized to enhance forest resilience to disturbances and environmental change. Thus, species were prioritized according to (1) their relative abundance in the region, selecting the less abundant as a means to improving overall biodiversity (Table F.1), (2) their tolerance to drought, selecting the most drought-resistant (Table F.2), and (3) their vulnerability to pest, selecting the less pest-prone (Table F.2). Hereafter we refer to these selected species as biodiversity enhancer, drought tolerant, or pest resistant, respectively. We did not apply any social neither economic criteria to prioritize species selection as we were especially interested on fostering forest resilience to disturbances rather than improving financially value of forest. In total, we simulated 33 management scenarios: 11 strategies (Table 3.1) × 3 species selection criteria, running each scenario only once. In all scenarios, all planted trees were considered to be instantaneously mature (we did not consider any temporal element in our simulation).

Table 3.1: Code for the 11 management strategies identifying the amount of area to be managed and the type of target patch to be functionally enriched or the type of plantation.

Strategy		**Area target to be managed (ha) or number of trees to be**		
		10 000	**40 000**	**70 000**
Functional enrichment	**Low Connected**	LowC10		
	High Connected	HighC10		
	Less Diverse	LessD10	LessD40	LessD70
Plantation	**Random**	Rand10	Rand40	Rand70
	Riparian	Ripa10	Ripa40	Ripa70

To test landscape behaviour to natural and anthropogenic disturbances, we simulated an episode of drought induced mortality, a severe generalized insect outbreak, and an intensive harvesting event. We imposed a 20% drought mortality, that is twice the rate of a catastrophic drought (Anderegg *et al.*, 2012). Species died according to the drought tolerance index, but corrected so that less tolerant species died up to seven times more than the most tolerant species (following Gustafson & Sturtevant, (2013)). Thus, the two species least tolerant to drought, *Abies balsamea* and *Tsuga canadensis*, had only a 50% chance of survival. The widespread outbreak killed up to 75% of all the pest-vulnerable species (Table F.2). We assumed then that different pest species (e.g. spruce budworm, emerald ash borer, brown spruce longhorn beetle, forest ten caterpillar, and butternut canker) severely affected the region at the same time, which may not be currently realistic but may occur in the near future (Logan *et al.*, 2003). The harvesting was done by clear-cutting and affected 10 000 ha of forest (but never recent plantations) and cuts were preferably allocated close to urban areas.

3.3.5 *Comparing landscapes*

We computed the five properties related to forest landscape resilience for the functional networks corresponding to the 33 simulated landscapes. Each network property of the simulated landscapes was compared by a log response ratio (LRR) to the same property of the reference landscape. This comparison was done for non-disturbed networks and under each disturbance (drought, pest outbreak, and timber harvesting). The five properties were also plotted in a radar-chart with fixed minimum and maximum values: *PC* and *Q* had default minimum (0) and maximum (1) values, while for *RD*, *FR* and BC^{PC} indexes, these were set at the absolute minimum and maximum values among all the networks, [0.281, 0.301], [0.895, 0.905] and [0.37, 2.67] respectively.

3.4 Results

3.4.1 Resilience properties of the reference and simulated landscapes

The reference landscape showed a high functional redundancy of 0.904 (maximum value is 1) but an overall response diversity of only 0.284, meaning that the current Central Quebec region is not functionally rich forest landscape but enough resistant to biodiversity loss because of the high functional redundancy. The connectivity of the functional network representing the reference landscape was reasonably high (0.68 over the range [0,1]) meaning that was feasible and quite fast to traverse the network from any pair of random nodes. However, modularity was very low (or even inexistent), with a value of 0.23 < 0.3, the lower limit for modularity detection. That is, the network was not spatially structured in modules of highly interconnected forest patches but loosely connected with patches of other modules. Network mean centrality index was 1.29, indicating than a most of the patches are peripheral (Figure 3.2).

With both functional enrichment of forest patches and adding up new forest patches via forest plantations on the landscape, response diversity slightly increased (to the range [0.286, 0.288]) while functional redundancy showed a negligible decrease (Figures 3.4A and 3.4B; see Annex G for the values of the five properties of all the networks). In general, these two indexes always followed contrasting trends: if diversity goes up, redundancy then is forced down (Table G.1). As more area was managed, response diversity of the landscape increased no matter the strategy. But, for any target area managed (Table 3.1), the functional enrichment strategy reported the highest increases. In particular, enriching the less functionally rich nodes was the most effective strategy, as it gave the highest response diversity increase per managed area. Both drought tolerant species and biodiversity enhancer species contributed to response diversity more than pest resistant species (Figure 3.4A).

Functional connectivity improved under both management strategies, being greater as more areas were managed (Figure 3.4C). The increase in landscape connectivity was similar no matter the strategy: new plantations did not appreciably increase connectivity more than enriched forest patches. Indeed, at 10 000 ha of target area, the most effective strategy for increasing functional connectivity was to enrich the less functionally rich nodes, rather than enriching high or low connected nodes or adding new patches via plantations (Figure 3.4C, Table G.1). When biodiversity enhancer species were used when applying the different management strategies, connectivity was in general less favoured, likely because most of these species could not disperse over long-distances (Table F.1). The addition of new forest patches did not contribute to landscape modularity. Indeed, only when current forest patches were enriched with pest-resistant species did the modularity indicator increase slightly (from 0.23 up to 0.28; Table G.1). However, it still remained very low (< 0.3) ensuring that the landscape was organized in modules (Figure 3.4D). In enriched landscapes, many new functional links appeared, so central nodes (network connectors and/or hubs) strengthen their structure. Functional enrichment was specially designed to reinforce the functional diversity flow across networks, especially when poorly connected and less diverse nodes were treated (Figure 3.4E). At a fixed level of target area, central nodes were less abundant in planted than enriched landscapes, likely because only a few new plantations strategically allocated would become connectors of the network. Species selection criteria did not affect node centrality (Figure 3.4E).

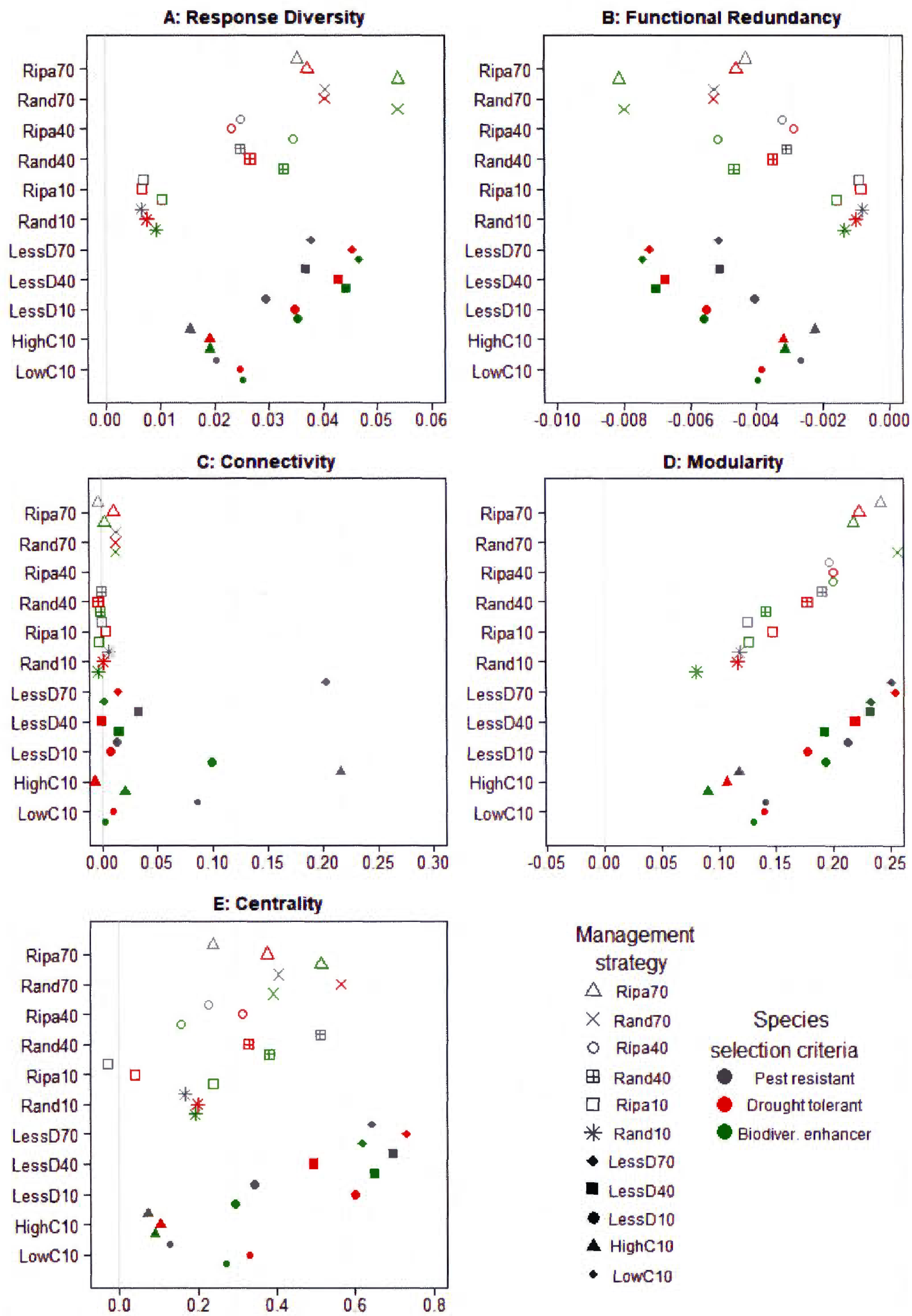

Figure 3.4: Log response ratio of response diversity (A), functional redundancy (B), connectivity (C), modularity (D), and mean generalized betweenness centrality index (E) between the 33 managed networks and the reference network.

3.4.2 Forest disturbances in the reference landscape

Response diversity and functional redundancy, the two properties directly associated to species functional traits, were negatively affected by the pest outbreak (but not by drought) and, as we hypothesised, did not vary following harvesting (Figure 3.5). Mostly harvesting, but also the pest outbreak, reduced network functional connectivity, but drought episode did not, and even had a tendency to increase connectivity (Figure 3.5, Table G.1). Modularity was invariant under any disturbance. The potential centrality of nodes was on average diminished by pest outbreak (Table G.1), compromising the dynamic flow across the network. Globally, both pest outbreak and harvesting greatly affected the backbone of the network (compare Figures 3.2 and G.2 and G.3), either by reducing the functional richness of the nodes or by eliminating some nodes, and consequently altering its structure.

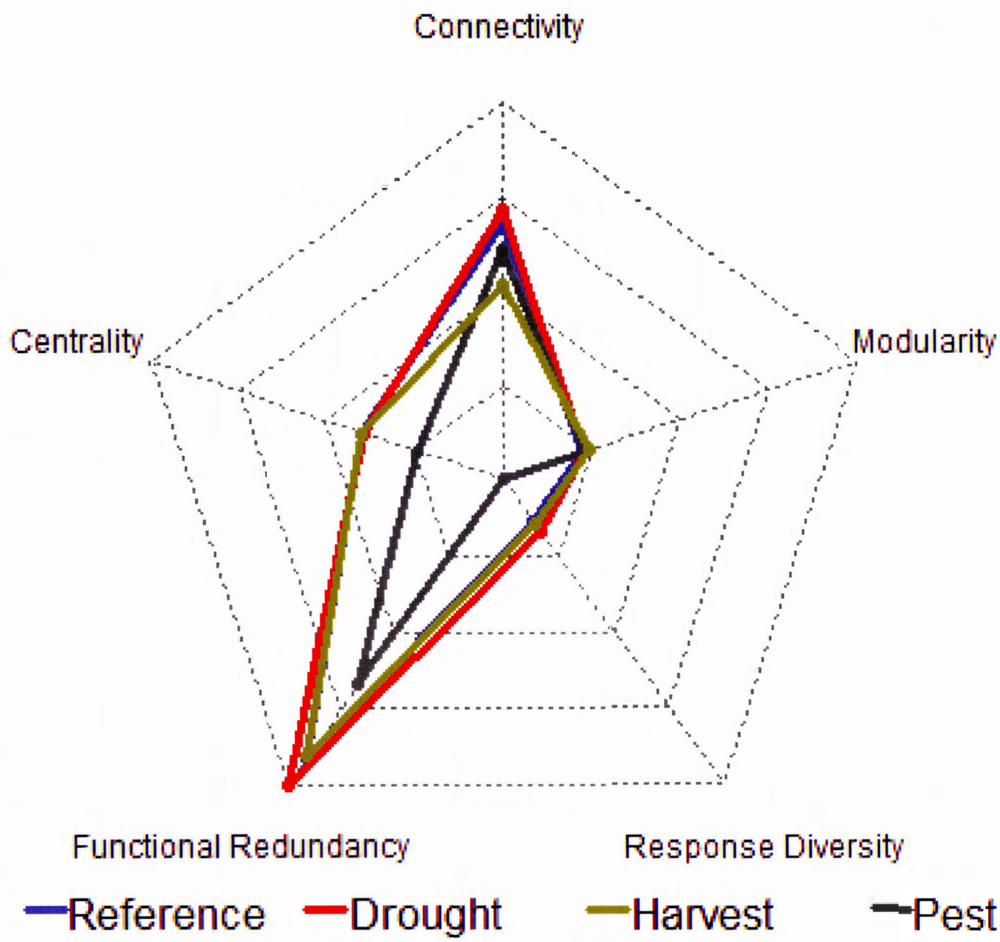

Figure 3.5: The five resilience associated properties for the functional network of forest patches of the reference landscape, and once it was disturbed by drought, pest and harvest episodes.

3.4.3 Response of the simulated landscapes to disturbances

All 33 proposed management scenarios (combinations of 11 strategies × 3 species selection criteria) reduced tree mortality by natural disturbances (drought and insect outbreak). Functional enrichment strategies were in all cases more effective in coping with natural disturbances than strategies where new forest patches were added (Table 3.2). This was especially true when the less functionally diverse patches were enriched with pest resistant species. Indeed, when both functional enrichment and new forest patch management strategies prioritised pest resistant species, pest-induced tree mortality was on average reduced by half compared to using drought tolerant or biodiversity enhancer species (Table 3.2). Comparatively, drought tolerant species were less effective in mitigating mortality. Drought tolerant and biodiversity enhancer species similarly contributed to reducing both drought-induced and pest-induced mortality, regardless of the management strategy implemented (Table 3.2).

Table 3.2: Percentage of trees killed by a simulated drought and a pest outbreak in the reference landscape and in the 33 managed landscapes (combining two management strategies (Table 3.1) and a three species functional trait selection criterion, B stands for the biodiversity enhancer, D stands for the drought tolerant, and P stands for the pest resistant, respectively). Differences between the drought- and pest-induced mortality for each of the 33 managed landscapes are also shown.

Treatment		**Disturbance**		**Differences**	
Strategy	**Criterion**	**Drought**	**Pest**	**Drought**	**Pest**
Reference		25.8	27.9		
LowC10	B	23.0	24.5	-2.8	-3.4
	D	22.8	24.3	-3.0	-3.6
	P	23.4	21.8	-2.4	-6.1
HighC10	B	23.9	25.5	-1.9	-2.4
	D	23.8	25.5	-2.0	-2.4
	P	24.0	23.8	-1.8	-4.1
LessD10	B	22.1	23.3	-3.7	-4.6
	D	21.9	23.6	-3.9	-4.3
	P	22.5	20.0	-3.3	-7.9
LessD40	B	20.6	21.6	-5.2	-6.3
	D	20.3	21.0	-5.5	-6.9
	P	21.1	16.5	-4.7	-11.4
LessD70	B	20.3	20.9	-5.5	-7.0
	D	19.9	20.7	-5.9	-7.2
	P	21.0	15.9	-4.8	-12.0
Rand10	B	24.0	25.8	-1.8	-2.1
	D	23.8	25.6	-2.0	-2.3
	P	24.3	23.5	-1.5	-4.4
Ripa10	B	23.9	25.9	-1.9	-2.0
	D	23.8	25.9	-2.0	-2.0
	P	24.3	23.5	-1.5	-4.4
Rand40	B	23.9	25.6	-1.9	-2.3
	D	23.8	25.8	-2.0	-2.1
	P	24.2	23.5	-1.6	-4.4

Ripa40	B	24.0	25.7	-1.8	-2.2
	D	23.8	25.8	-2.0	-2.1
	P	24.2	23.5	-1.6	-4.4
Rand70	B	23.6	24.8	-2.2	-3.1
	D	23.5	25.2	-2.3	-2.7
	P	24.0	22.8	-1.8	-5.1
Ripa70	B	23.6	25.3	-2.2	-2.6
	D	23.6	25.6	-2.2	-2.3
	P	24.1	22.9	-1.7	-5.0

Because harvesting did not modify species richness in forest communities, both response diversity and functional redundancy were stable in all harvested landscapes (Table G.1). Connectivity was systematically reduced under timber harvesting (Table G.1). Nonetheless, all strategies prevented to some extent the loss of connectivity, although enriched landscapes better mitigated connectivity loss due to harvesting (Figure 3.6). Pest outbreak consistently reduced functional redundancy and response diversity in simulated landscapes (the latter still being higher in functionally enriched landscapes than in planted landscapes) (Table G.1). However, both strategies could mitigate response diversity loss under a pest outbreak (Figure 3.6). On the other hand, drought did not substantially alter either response diversity or functional redundancy of simulated landscapes (Table G.1), suggesting that overall functional diversity was less affected by a drought episode. Landscape connectivity behaved similarly when disturbed by either drought or a pest outbreak, and a functional enrichment strategy prevented the loss of central nodes (against all types of disturbances) more than plantations strategies did (Figure 3.6).

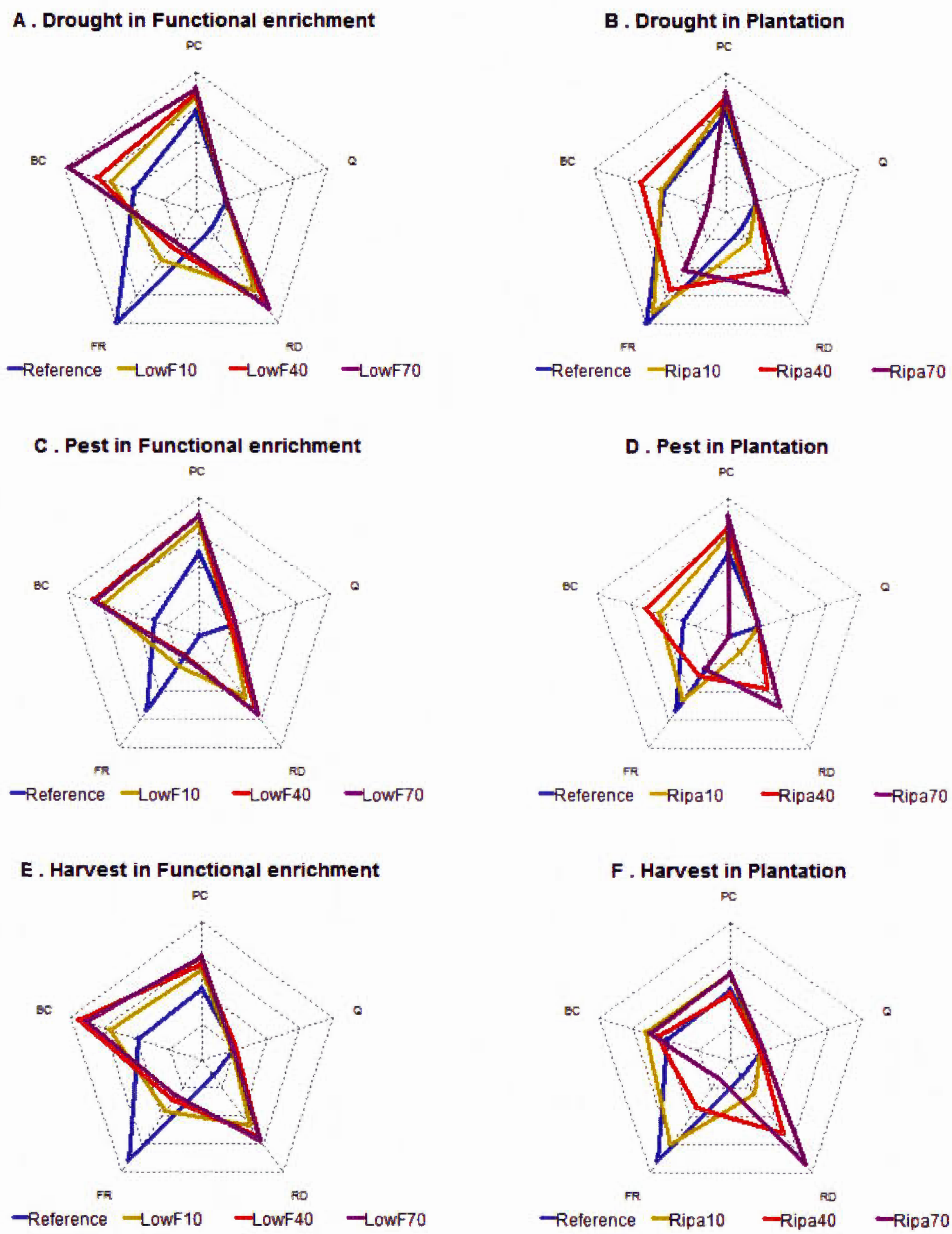

Figure 3.6: The five resilience associated properties: response diversity *RD*, functional redundancy *FR*, connectivity *PC*, modularity *Q*, and mean generalized betweenness centrality index BC^{PC} for the functionally enriched (A, C, and E) and the planted landscapes (B, D, and F) affected by drought (A and B), pest outbreak (C and

D), and timber harvesting (E and F). The selected species were drought tolerant, pest resistant, and biodiversity enhancer for the simulated landscapes affected by drought (A and B), pest outbreak (C and D), and timber harvesting (E and F), respectively. In all radar plots the reference network has also been affected by the corresponding disturbance.

3.5 Discussion

Our innovative approach links two tree-level properties (response diversity and functional redundancy) and three landscape-level properties (connectivity, modularity and centrality), which all contribute to forest landscape resilience. Indeed, by combining forest functional diversity indicators and forest network topology characteristics, we could better account for resilience at the landscape scale. Moreover, this generic, broad-scale quantification of resilience could be extended to any ecosystem (as all are organized around interrelated components). We have applied it to a temperate rural landscape in south-eastern Canada. First, we were able to quantify critical resilience components of this forest ecosystem, but even more meaningful, we explicitly used this functional-network approach to quantitatively compare the response and variability of the five ecosystem resilience properties and overall resilience to different management strategies and disturbance regimes.

We specifically compared two management strategies: functional enrichment of current forest patches versus addition of forest patches by planting polycultures across the landscape. Our simulations and analyses led us to conclude that functional enrichment of the less functionally diverse patches was the best management option to enhance resilience at the landscape scale. At a fixed level of management intensity (e.g. 10 000 ha), we found that targeting the most functionally poor patches gave the highest increase in response diversity, as expected, but functional connectivity benefitted most, even more than targeting low/high connected nodes or adding new forest patches. In addition, functional enrichment, especially of less diverse forests, was also the most cost-effective strategy to cope with natural disturbances (drought and pest outbreak). Promoting functional diversity appears to be the most efficient management strategy for increasing overall forest resilience to disturbances. As forest patches become functionally richer, they then become potential sources of higher diversity that in turn positively reinforce the system through dispersion (Martín-Queller & Saura, 2013).

We therefore could verify our first hypothesis that forest management improved functional response diversity of this fragmented forested rural landscape with the trade-off that functional redundancy slightly decreased. Because both management strategies (enrichment and plantations) increased the presence of biodiversity enhancer, drought tolerant, or pest resistant species that were not particularly dominant in the reference landscape, the new planted species could notably contribute to improving forest diversity. Indeed, in all scenarios, response diversity showed the greatest improvement when biodiversity enhancer species were promoted. Yet, we thought that by adding new forest patches via pluri-specific plantations we would contribute to landscape connectivity more than by enriching current forest patches, but this was not the case. Instead, we showed that at a low management intensity (e.g. 10 000 ha), functional connectivity was better reinforced when poorly diverse patches were managed, and at moderate and high intensities, the effect on connectivity was similar under both management strategies (Figure 3.4). Interestingly, the pest-resistant tree species in our study tended to have a larger dispersal area than the drought tolerant or biodiversity enhancer tree species as connectivity was greatly improved when pest-resistant species were added.

We confirmed that timber harvesting did not alter either response diversity or functional redundancy, but modified landscape configuration as both network connectivity and centrality were negatively affected. Further, even by using our best management strategies to increase resilience through functional enhancement or addition of new forest patches, we could not maintain former levels of connectivity or centrality. As well, we confirmed that pest outbreak greatly alters the landscape, not only by diminishing functional diversity but also reshaping the topology of the network as most of the connections are lost. Pest control, including monitoring and mitigation measures, as well as the planning of sustainable harvesting levels that take into account potential future disturbances should be mandatory management directives to sensibly contribute to forest landscape resilience.

Network modularity, that is, the topological organization of network elements into groups of elements highly interconnected among them but loosely connected with elements of other groups was not relevant neither in the reference landscape neither in the managed ones. In the reference landscape, the spatial arrangement of forest patches did not follow any specific modular pattern, but the spatial distribution of forest species (and the corresponding functional diversity) neither. Both types of plantations, riparian and at random, were not designed to improve the modularity of the network and were therefore scattered across the landscape (Figures F.3 and F.4). The functional enrichment of forest patches was not structured to reinforce network modularity, but simply targeted either poorly connected, highly connected, or functionally poor patches that were also heterogeneously distributed on the territory. Thus, any of the management strategies could indirectly alter the non-modular character of the reference landscape.

3.5.1 Limitations and further research

One obvious limitation of this study is the static nature of our evaluation. All planted trees in either current or new forest patches were considered mature and ready to disperse their seeds. Although this approach is a very useful first step to evaluate the potential impact of various planting strategies to increase the overall resilience of forest patches in a rural landscape, further work will need to implement a more dynamic approach. Such a dynamic modelling approach will allow us to determine (1) how the five resilience properties vary over time as a forest re-organises following various types of disturbances, (2) how tree communities regenerate after disturbance, but even more relevant, (3) if the forest is better adapted to cope with multiple types of interacting disturbances. Ultimately, we could observe the added value of these types of management strategies over time under various scenarios of climate change and invasive harmful insects and disease, and not only at a static point in time.

The study of the adaptability of future tree communities to uncertain future conditions and how management can enhance forest ecosystems adaptation is still a major socio-ecological issue (Messier *et al.*, 2013; Puettmann, 2014). Yet, to address these questions, it will be necessary to develop modelling frameworks that can integrate, at the right spatio-temporal scales, the interactions between climate, vegetation, disturbances, and biochemical processes (Keane *et al.*, 2015), simulate how the system responds to different management and planning scenarios (Parrott *et al.*, 2012), and quantify explorative scenario storylines and their associated uncertainty (Peterson *et al.*, 2003; Rounsevell & Metzger, 2010). The next step in our research will be to adopt a dynamic and spatially explicit landscape modelling approach to include essential vegetation dynamics processes, mainly post-disturbance regeneration, growth, and mortality, all subject to future climatic changes, to study long-term forest landscape resilience.

Network theory supports interpretation of hierarchical, interconnected, complex ecosystems. Network analysis has actually proven to be a valuable approach for depicting resilience of socio-ecological systems when faced with perturbations, highlighting weaknesses and strengths, and potential maladaptations (Macfadyen *et al.*, 2011; Moore *et al.*, 2015). However, forest landscape resilience from a network perspective has been poorly explored (but see work by Craven *et al.*, (2016)). Therefore, we advocate a holistic multi-dimensional approach that captures forest landscapes as spatial entities as well as essential drivers of forest ecosystem resilience to natural and/or anthropogenic disturbances.

3.6 Acknowledgments

We thank Melanie Desrochers for providing GIS data and support.

CONCLUSION

The main objectives of my thesis were twofold. Firstly, to develop methodological approaches for exploring how forest ecosystems respond to resilience-target management regimes and disturbances. Secondly, to provide guidelines for managing for resilience on highly anthropised forest landscapes facing global changes, notably shifting natural disturbance regimes. The methodological approaches developed in the framework of this thesis are intended to (1) capture the complexity of forest landscapes where human presence exert multiple pressures, (2) quantitatively explore landscape-scale management regimes for forest landscapes in an uncertain global change context, (3) test the response of the system to current or future natural disturbance regimes, (4) work at the landscape level rather than the stand level so the management strategies applied can effectively shape natural disturbance regimes, and (5) explicitly quantify ecosystem properties directly related to resilience to disturbances.

To address these challenges, I developed a generic demand-allocation procedure to model land-use/land-cover transitions. Chapter 1 provides the foundation of this new procedure and its use as the core of a spatially explicit land-use change model to mimic three main land transitions in a Mediterranean landscape. To investigate the potential of land-cover changes as a management option for shaping fire regimes in that Mediterranean landscape, Chapter 2 outlines how I coupled this land-use change model to an existing fire-succession model. Finally, Chapter 3 presents an innovative multi-scale evaluation of forest resilience to natural and anthropogenic disturbances based on the functional response traits of different species and forest network topological features. I applied this approach in south-eastern Canada to evaluate whether a) functional enrichment of current forest patches or b) increased landscape connectivity enhances resilience of an agro-forested landscape.

The demand-allocation land-use change model

As outlined in Chapter 1, a major objective was to develop a generic spatially explicit demand-allocation procedure to mimic land-use/land-cover changes. In a demand-allocation approach, the demand or quantity of change is an input of the model (i.e. defined by the user) whereas the spatialization of that amount of change is the essence of the procedure. **My allocation procedure focuses on land transition processes** (e.g. rural abandonment) rather than on land-cover types (e.g. croplands vs. forest), **and considers land-cover changes as a complex process with self-organization properties**, such as fires or contagious diseases (Ward *et al.*, 2000). This means that, firstly, the procedure is not rule-based at the cell-state level (as cellular automata approaches are (White & Engelen, 1993)), but rules are defined at the land transition level. Secondly, spatial patterns of change emerge from simple rules of land change origination and contagion. This allocation procedure is to be used in conjunction with a transition-potential map that accounts for the spatial likelihood the target land transition occurs. Uncertainty related to land-cover changes is then incorporated in the modelling framework through these transition potential maps and the stochasticity associated with the rate patches of change emerge and grow.

This new demand-allocation procedure was embedded in MEDLUC, a modelling framework designed to simulate land-use/land-cover changes in Catalonia (NE Spain). I calibrated MEDLUC to replicate the urbanization, rural abandonment, and agricultural conversion processes which occurred in Catalonia between 1993 and 2009. The transition-potential map of each land transition (e.g. rural abandonment) was initialised as the neighbour factor (see Verburg *et al.*, (2004)) of the target land-cover (e.g. scrublands). Such initialization was acceptable enough to simulate urbanization and rural abandonment in Catalonia (the two most abundant land transition processes during the targeted period of time). This simple definition of the transition-potential maps assumes that land conversions tend to occur close to zones where the target land-cover prevails. Thus, land-use/land-cover changes seem to favour land-cover aggregation and overall landscape mosaic homogenization (Stellmes *et al.*, 2013). Additionally, one could argue that transition-potential maps that include many social and environmental variables for their initialization are often dispensable (Mas *et al.*, 2004; Soares-filho *et al.*, 2013). Instead, **transition-potential maps that only depend on landscape configuration variables would be of greater benefit if the land-use/land-cover change model explored plausible futures** (Mas *et al.*, 2014). If this were the case, transition-potential maps would be systematically (and automatically) updated as land transitions occurred by the modelling framework itself. Otherwise, future projections of the explanatory social and environmental variables would be required, and may not necessarily be available or reliable. Therefore, the land-use/land-cover change model **MEDLUC is an excellent tool to downscale supra-national land-cover demands to the regional scale, and requires little information about drivers of land-transitions to forecast land-change spatial allocation.**

Exploring interactions between land-cover changes, fire, and vegetation with a landscape dynamic meta-model

Chapter 2 examined whether agricultural conversion of natural and semi-natural lands to croplands in a Mediterranean fire-prone landscape could shape its own fire regime. Fire incidence reduction due to an increase of agricultural land in the landscape is possible through a combination of three factors: the amount of highly-burnable fuel becomes reduced (and consequently fire intensity), the continuity of these fuels is disrupted, and accessibility to fire fronts is facilitated, so fire brigades are better able to rapidly reach a fire and suppress it. Overall, to quantify the effect of agricultural conversion on fire regimes, I measured the fire suppression effectiveness at the fire level as the ratio between the area effectively suppressed and the target area to be burnt.

Chapter 2 revealed three main findings from the analysis of the spatio-temporal interactions between agricultural conversion, fire behaviour, and fire suppression. Firstly, the relationship between the amount of new agricultural land (i.e. demand) and fire suppression effectiveness was not linear. This was especially evident when agricultural conversion followed an aggregate pattern. At low annual demands, fire suppression effectiveness remained almost constant, then it sharply improved at a higher demand, but subsequent demand increases did not result in a significant benefit to fire suppression. This means that **(1) a considerable land conversion effort is required to change the connectivity pattern of highly-burnable fuels and therefore shape the fire regime in Catalonia, and (2) once the landscape is no longer fire prone, land management can no longer influence the fire regime?** Secondly, to achieve the same level of suppression, less management effort was required when agricultural land was aggregated, rather than scattered. Fire suppression effectiveness was, in most cases, greater when **larger new agricultural patches interrupted highly-burnable fuels more efficiently**. Moreover, aggregated agricultural land better prevented the loss of forest core area. Thirdly, there is **a time lag between the implementation of the landscape management policy** (e.g. agricultural conversion) **and the desired effect** (e.g. reduction of fire incidence). Indeed, the length of the time lag depends on the intensity of the management action (e.g. annual amount of land converted to agricultural land). Thus, when implementing these kinds of interventions, outcome monitoring needs to be managed over the long term.

The development of the landscape dynamic meta-model outlined in Chapter 2, **is one of the first attempts to include large scale impacts of human activities on Mediterranean forest landscapes** (There has been a recent extension for LANDIS-II to integrate land-use changes in temperate forests (Thompson *et al.*, 2016)). My meta-model captured the complex human-natural dynamics of the Mediterranean fire-prone landscape under study, quantified and compared the outcomes of alternative landscape-scale management regimes for shaping the fire regime, and provided a spatial scale suitable for guiding management policies to reduce the occurrence of large high-intensity fires in the Mediterranean. When coupling both models (the land-use change and the fire-succession), fire was the bridging element. Fire spread was sensitive to fuel content of the different land-cover types, but what is more relevant is my design for a fire suppression strategy which takes into account the changes on landscape configuration. **As a result of my meta-modelling approach, we can, for the first time, quantify the contribution of new agricultural land on strengthening fire fighting capacity, and thus on controlling the fire regime of a fire-prone region.**

Functional traits and network properties to characterise ecosystem resilience

Chapter 3 focused on quantifying five forest ecosystem resilience related properties (e.g. response diversity, functional diversity, network connectivity, modularity, and centrality) of a temperate agro-forested landscape of south-eastern Canada (hereafter the reference landscape). I also investigated the variability of these properties under two management strategies (functional enrichment and polyculture plantations) and under three disturbances (drought, insect outbreak, and timber harvesting) affecting the reference and all the simulated landscapes. Actually, both management strategies were implemented at three rates of area managed (low, medium, and high), and combined with three trait-based criteria (e.g. drought tolerant, pest resistant, and biodiversity enhancer).

First of all, the management scenarios were all successful in increasing the response diversity of the reference landscape, becoming higher as area managed increased. The increase in functional diversity was offset by a slight loss in functional redundancy. These two metrics always varied in opposite directions. Functional enrichment (at low and medium rates) contributed more than plantations to increases in response diversity. In particular, enriching functionally poor patches was the most efficient strategy for improving response diversity. Landscape connectivity was similarly enhanced under both management strategies. However, enriching the less functionally rich patches was again the best cost-effective option. Centrality of the network backbone was also favoured by the enrichment of current forest patches rather than through new plantations. Therefore, **functional enrichment of functionally poor patches was the most successful strategy in enhancing overall ecosystem resilience to disturbances**. On one hand, when testing the reference and simulated landscapes to disturbances, using pest resistant species reduced, on average, a quarter of the pest-induced tree mortality. However, drought tolerant species reduced about half of tree mortality during a drought episode. Indeed, biodiversity enhancer species performed as well as drought tolerant species in coping with natural disturbances. On the other hand, the functional enrichment based management scenarios were better in coping with disturbances than were plantations. Thus, **mitigation / preventive treatments of current forest stands to potential pest attacks should be quite effective** (as long as it would be feasible to forecast the target insect pest or disease). But **to unknown / unpredictable environmental changes, fostering functional diversity is for now the best option**.

In Chapter 3, **I developed a unique and innovative approach that links two tree-level properties and three landscape-level properties, all of them potentially influencing forest landscape resilience to disturbances.** This multi-evaluation of forest landscape resilience bridges (1) the capacity of tree species to cope with disturbances and new environmental conditions, characterised through target response functional traits and (2) the role landscape composition and configuration plays in fostering resistance and adaptability, characterised through the topological properties of the forest network. Thus, **I used five metrics (response diversity, functional redundancy, network connectivity, modularity, and centrality) as indicators of forest ecosystem resilience**. To support the resilience analysis, **I synthesised the five indicators into a standardised pentagon display to compare the effect of management and disturbances all at once on the whole set of indicators**. This pentagon display clearly presents the overall management trade-offs and the ecosystem weakness. By incorporating response diversity and functional redundancy in resilience evaluation, we gain insights into the prevalence of functionally similar / dissimilar species giving stability to the ecosystem versus making it more vulnerable to environmental change. By combining both metrics, it is possible to elucidate how ecosystem functioning and thus ecosystem services provisioning may vary in response to management actions and disturbance impact (Cadotte *et al.*, 2011). But because forest landscapes are fundamentally assemblages of heterogeneous spatial entities (i.e. forest patches) interconnected through wind, water, moving organisms, or humans (that transport biological material), network theory can clearly contribute to discovering which landscape configurations are more resistant to some types of disturbances, and when cascading failures are more likely (Albert *et al.*, 2000; Barthélemy, 2011).

Management implications

All taken together, the modelling approaches that I have developed at the landscape level can help to improve the management of fire-prone landscapes. Indeed, alternative landscape resilience management strategies have been proposed and evaluated in Chapters 2 and 3 for the Mediterranean fire-prone region of Catalonia and the fragmented agro-forested landscape of south-eastern Canada, respectively. Here, instead of providing or discussing precise management guidelines or schemes for each of the study areas of this thesis, I will highlight some issues to be aware of when managing forest landscapes in an uncertain changing context: spatial legacies, dynamic monitoring, and trade-offs. These issues have arisen from observations in the two investigated systems and in related studies. Firstly, the need to emphasise the importance of long-term studies for understanding both the legacies and cumulative effects on forest ecosystems of management practices currently being applied (James *et al.*, 2007). As we know, footprints on ecosystem structure, composition, and function of silvicultural treatments can persist over centuries. Secondly, when analyzing the outcomes and impacts of a management plan, rather than looking only at a benchmark future (e.g. a snapshot in 2050 or 2100), try to focus on the trajectory of the system at shorter time intervals until reaching the target time horizon (Morgan *et al.*, 2007). This will allow for the detection of critical thresholds of the system that could otherwise go undetected. In Chapter 2, by analyzing the fire suppression capacity every five years under different landscape-scale agricultural conversion strategies, I could identify the time required (or equivalently, the amount of land change) to effectively strengthen the fire fighting system through a more disconnected, less fuel-loaded landscape. Thirdly, to recognise that significant trade-offs exist between specific practices for creating forest ecosystems more resistant to natural disturbances, and the overall mitigation directives to enhance system resilience to climate change and potential unknown environmental conditions (Côté & Darling, 2010). For example, the agricultural conversion strategies proposed in Chapter 2 were actually successful in reducing fire effects, but little is known about either the impact on key forest ecosystem services or on biodiversity, and may also conflict with bioenergy policies. In Chapter 3, increasing the presence of pest-resistant species was the most suitable treatment in the face of this imminent threat, but overall resilience of the system may be compromised if other response traits are not also boosted. Lastly, whenever possible adopt a participative scenario, collaborating with stakeholders, local agencies, and/or regional governments (Sturtevant *et al.*, 2007). This ensures that perceptions from experts, the scientific community, and decision-makers about possible future scenarios are somewhat taken into account. But most importantly, modellers and analysts can be involved during the whole process, exchanging information with the participants about the assumptions being made, the uncertainties being incorporated, and the limits of the modelling approach adopted (Parrott *et al.*, 2012; Van Berkel & Verburg, 2012).

Limits of the methodological approaches

Spatially explicit landscape dynamic models presented in this thesis have been very helpful for testing hypotheses about pattern generation and interactions between natural and anthropogenic processes in forest landscapes, and in evaluating landscape-scale management scenarios to reduce exposure to forest wildfires. But this type of model does not consider individual agents as the driving force of system change. Purely agent- / individual-based approaches model the behaviour of individual heterogeneous agents with the capacity to evaluate a situation and its constraints and benefits, and make the best possible decision (Bonabeau, 2002). To move towards a more comprehensive understanding of the complexity of human-natural systems and be able to better inform natural resources management in a changing global context, modelling approaches have to move towards hybrid methods and/or pattern-oriented models (Grimm *et al.*, 2005; IPBES, 2016). In such approaches, bottom-up and top-down driving forces should be adequately balanced, interactions should occur across spatial, temporal, and hierarchical scales, new structures and/or agent behaviours should also be possible (Parrott, 2011). The new generation of ecological models should focus on the emergence of higher level processes and patterns from the behaviour and interactions of lower-level entities of the system. In addition, it is imperative that models no longer rely solely on observed empirical conditions and relationships. Otherwise, the scope of such models will continue to be restricted to explaining the current state and unable to forecast ecological responses under new environmental conditions (Grimm & Berger, 2016).

By using the multi-evaluation approach based on tree-level and landscape-level indicators, a holistic informative portrait of forest landscape resilience and its variability under different management scenarios and disturbances can be depicted. However, in Chapter 3 I did not simulate the evolution over time of tree communities within the agro-forested landscape. This has therefore limited our understanding regarding which management regimes were most effective in enhancing ecosystem adaptive capacity, and which disturbances lead to regeneration failures. The planted trees were new sources of functional diversity that could actually spread and regenerate in adjacent stands. A simulation of forest ecosystem dynamics (including processes of regeneration, growth, colonization, and mortality) would highlight the positive feedback effects over time of functionally enriching current forest patches.

Future research directions

Landscape dynamic models are promising approaches for investigating the complex interactions between vegetation processes (e.g. productivity, post-disturbance succession, mortality), natural disturbances (e.g. fires, diseases and insects, drought), and, whenever possible, biogeochemistry processes (e.g. evapotranspiration, nutrient dynamics). However, updates are needed in a global change context (Keane *et al.*, 2015). Firstly, landscape dynamic models should include the relevant effects of climate on all these processes, and secondly, anthropic activities altering forest ecosystems (e.g. forest management practices, land-cover transitions) should also be incorporated (Mayer *et al.*, 2016). Indeed, to capture the response of vegetation to new environmental conditions, mechanistic approaches that describe the biological, chemical, and physical relationships between vegetation and the environment (e.g. soil, climate) are preferable, rather than empiric models (Cuddington *et al.*, 2013). However, an unavoidable trade-off exists between including as many mechanistic details as possible and the level of model complexity achievable and the working scale. I propose updating the meta-model resulting from coupling the land-use change model MEDLUC and the fire-succession MEDFIRE (Chapter 2) by, firstly, including vegetation processes such as productivity, establishment, and mortality sensitive to climate. To achieve this, a new state variable tracking forest biomass would be required. Thereby, episodes of drought-induced mortality could feedback in fires, and vice versa, recurrent fires could feedback in vegetation regeneration capacity under water-stress conditions. Secondly, another consideration would be the designing and implementing of a forest management module to reproduce traditional sylvicultural interventions (e.g. commercial thinning, selection cutting, clear-cuts). It would be particularly interesting to implement European level bioeconomy related policies at the regional level (Scarlat *et al.*, 2015). Increasing biofuel demands are thought to be supported by Mediterranean agro-forested landscapes too. Lastly, another avenue for improvement would be the inclusion in the modelling framework of an increasingly important biotic disturbance affecting Mediterranean forests, the pine processionary moth (*Thaumetopoea pityocampa*), that is expanding its geographic range due to climate warming (Hódar *et al.*, 2003; Battisti *et al.*, 2005). This would enable not only the studying of the effects of defoliation on vegetation, but also the interactions with other disturbances.

In Chapter 3, I proposed precise metrics to quantify five properties related to forest resilience to disturbances, two based on species functional response traits, the other three on spatial network topology. We need further studies to investigate metrics and indicators for forest resilience, that allow us to capture and describe ecosystem adaptive and learning capacities and the system's ability to recover from pressures and perturbations. Also, it is essential that indicators can anticipate and prevent undesired regime shifts, able to detect a priori irreversible changes of system state. For forest landscapes, resilience indicators should account for the functional complexity of the system. Further research is needed to elucidate the mechanistic role of response and effect of functional traits of tree species on the overall forest ecosystem resilience. But again network theory could hold the key to offering a generic approach for detecting essential behaviours related to system resilience (Gao *et al.*, 2016).

One interesting, but not yet fully explored application of network models on forest-pathogens dynamics is the investigation of the potential spreading pathways of current or future outbreaks through host-tree patches, or even through transportation networks. Network-based studies tracking the spread of contagious human diseases at the local scale (by physical contact) and global scale (by travelling individuals) have provided important information to public health agencies (Meyers *et al.*, 2005; Colizza *et al.*, 2007). Similar approaches could be very informative for plant diseases (Jeger *et al.*, 2007). For example, it would be interesting to identify connectors and hubs in living plant trade networks that may require a particular control to avoid an epidemic (Harwood *et al.*, 2009). But more specifically, to dynamically model propagation of forest insects and/or diseases could help to identify critical connectivity thresholds, central nodes that control most of the spread, and potential dispersal routes across the network of host patches (Ferrari *et al.*, 2014).

ANNEX A

CALIBRATION METHODOLOGY - CHAPTER 1

We run the MEDLUC model over the Land Cover Map of Catalonia of 1993 to allocate the observed demand for urbanization, rural abandonment, and agriculture expansion transitions. We followed a combinatorial design to set the experiments. Each of one was characterized by a $\{\lambda_i, \lambda_s, k\}$ set, where the parameters took values in $\lambda_i = \lambda_s = \{0.05, 0.1, 0.25, 0.5, 1, 2.5, 5, 10, 15, 20\}$ and $k = \{0.1, 0.2, 0.3, 0.4, 0.5\}$. These experiments were run 50 times for both spatial resolutions, 1000 m and 100 m.

For each replicate of each experiment, histograms for the patches-of-change with multiplicative intervals for the bins were built (Pueyo 2006). We got 50 $\{s_j, \hat{f}(s_j)\}_j$ series, where $s_j = 2^{j+1/2}$ is the central value of bin j, and $\hat{f}(s_j)$ is the estimated probability density. We averaged the probability densities at the bin level to determine the mean probability density of each j bin, $\bar{f}(s_j)$. Scenarios were identified by the β exponent (again, fitted by linear regression) for the $\{s_j, \bar{f}(s_j)\}_j$ average distribution (Figure A.1). To find the maximum likelihood scenario we assessed the root mean squared error (*RMSE*), between the probability densities of the observed patches-of-change size distribution and the above average simulated distribution (Equation A.1):

$$RMSE = \sqrt{\frac{1}{m}\sum_{j=1}^{m}\left(\bar{f}(s_j) - f(s_j)\right)^2} \qquad [A.1]$$

where $f(s_j)$ is the observed probability density and $\bar{f}(s_j)$ the average of the simulated probability densities of bin *j*. We chose the scenario returning the lowest *MSE* as the best scenario replicating the observed patches-of-change size distributions.

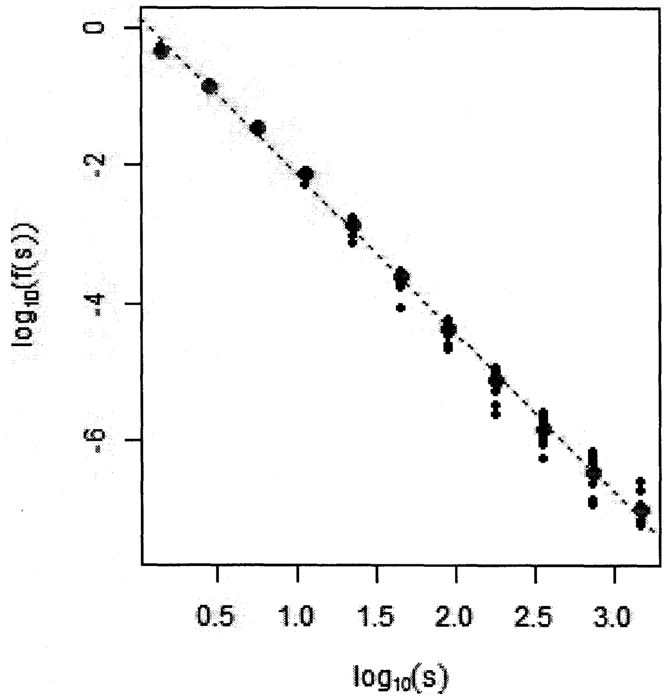

Figure A.1: Probability density function for each run in a log-log scale (grey diamonds) and the mean density for each bin (red dot). The regression line is fitted for the mean densities (red dotted line) and the slope is $\beta = 2.31$.

ANNEX B

COMPLEMENTARY RESULTS - CHAPTER 1

MEDLUC is a stochastic spatially explicit land-use / land-cover change model. For each scenario, multiple replicas will produce variable results. Here we show the likelihood of change for urbanization (Figure B.1), rural abandonment (Figure B.2), and agriculture expansion (Figure B.3) simulated at 1 km to replicate empirical demands of the 1993 - 2009 period. The likelihood is computed as the average of 100 replicas based on the MEDLUC spatial output describing the locations affected by a transitions. These three likelihoods are summarized as histograms (Figure B.4), showing a high allocation variability when simulating agriculture expansion (because there are no locations that regularly change) while there are a significant number of locations that often change under the urbanisation and rural abandonment processes.

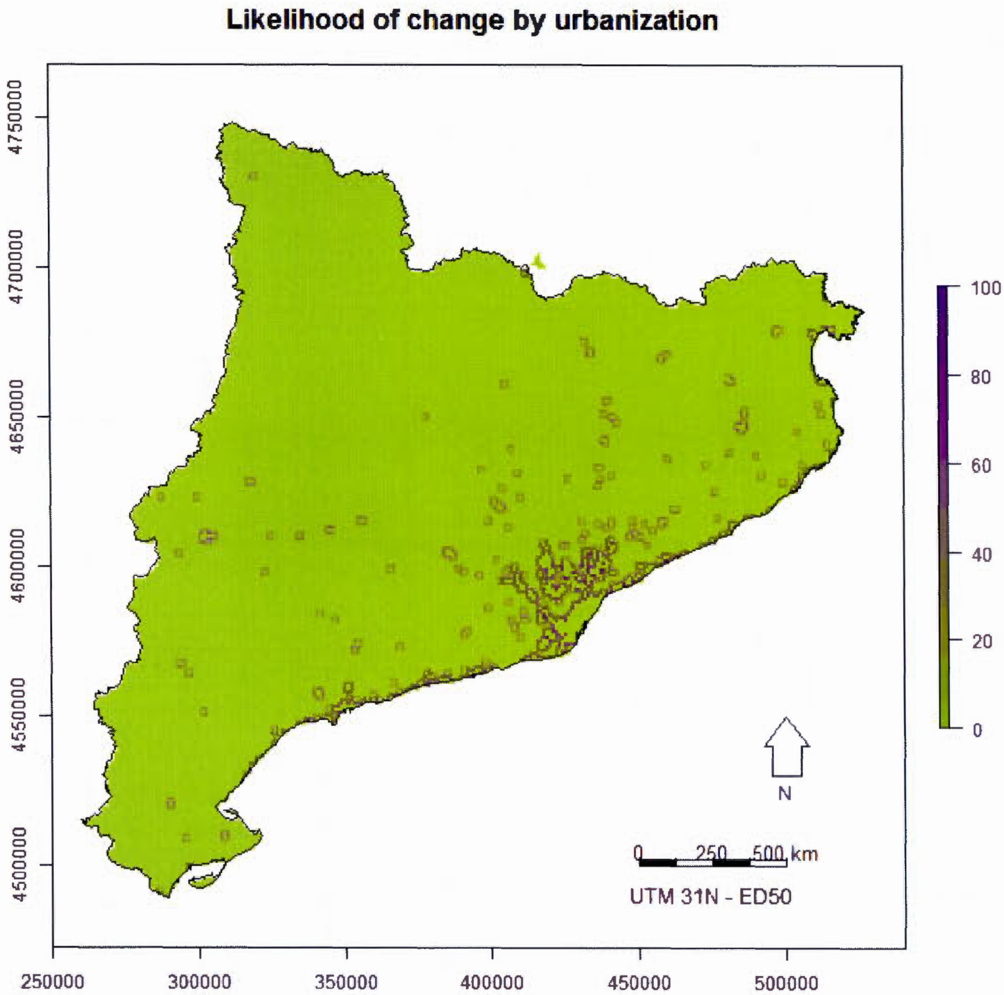

Figure B.1: Likelihood of change to urban areas in Catalonia as simulated by the MEDLUC model at 1 km^2 when allocating 579 km^2.

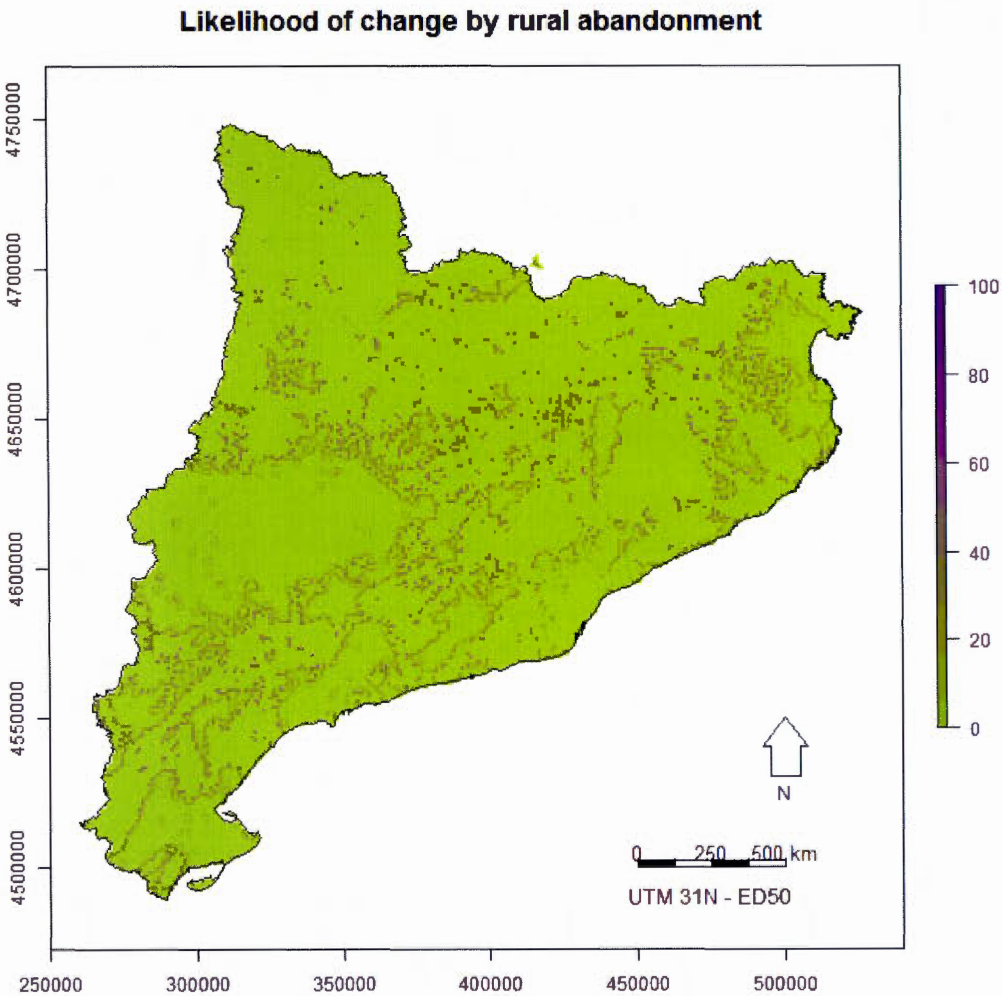

Figure B.2: Likelihood of change to natural and semi-natural areas in Catalonia as simulated by the MEDLUC model at 1 km^2 when allocating 1319 km^2.

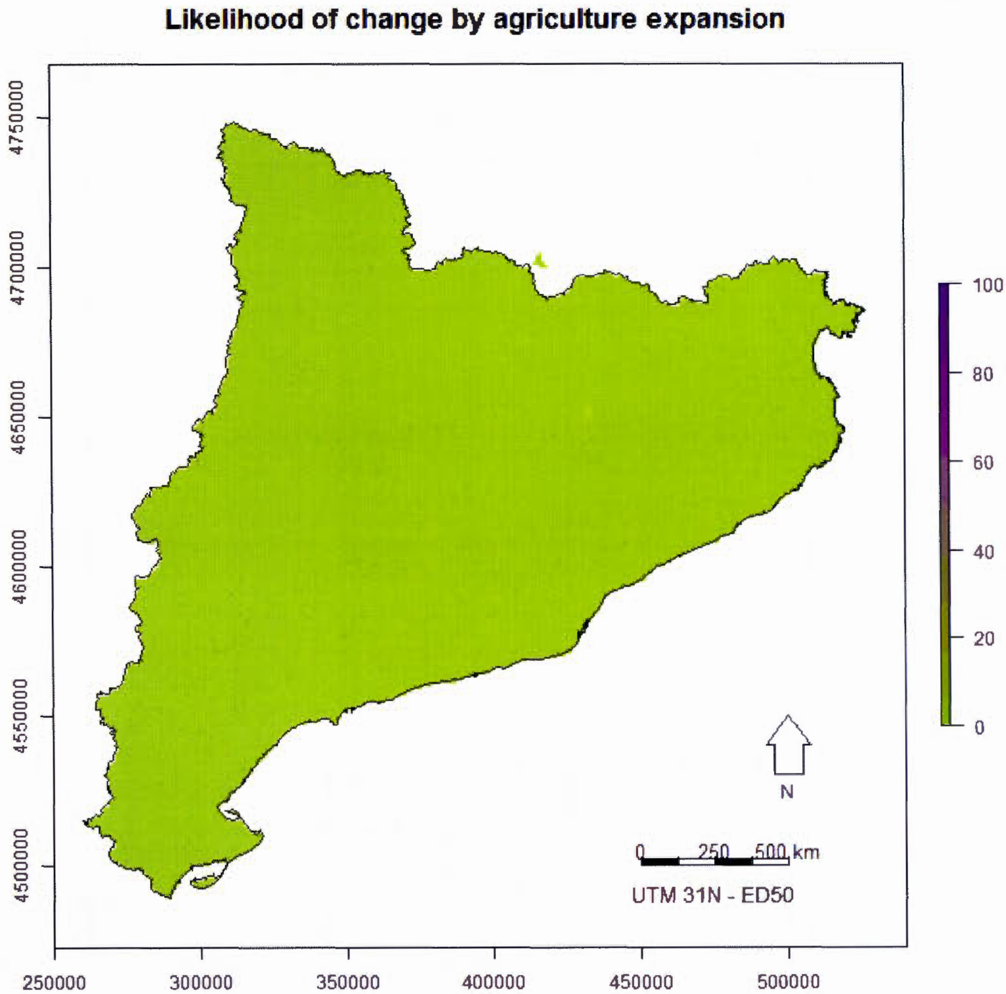

Figure B.3: Likelihood of change to agriculture land in Catalonia as simulated by the MEDLUC model at 1 km^2 when allocating 112 km^2.

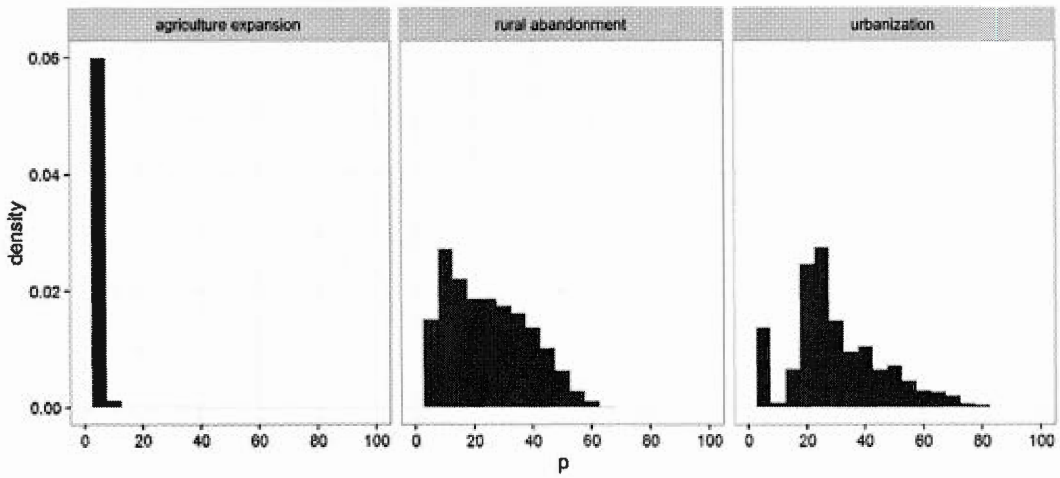

Figure B.4: Density histograms of the likelihood of change (greater than 0) for the three land-transitions simulated by MEDLUC at 1 km^2 in Catalonia.

ANNEX C

STUDY REGION: CATALONIA - CHAPTER 2

Catalonia is a 32 100 km^2 region situated in the NW of the Mediterranean basin, on the Iberian Peninsula. Catalonia has a mostly Mediterranean climate, with warm summers and mild winters, but the areas further inland have a more continental climate, with drier and hotter summers. Its orography affects the climate, with the Pyrenees in the north, an extensive plain in the west, and the multiple mountain ranges stretching along the coast, all contributing to a heterogeneous landscape mosaic. A strong precipitation gradient occurs along a north-south direction, going from mesic to more xeric conditions. Currently, 60% of the territory is occupied by natural and semi-natural land, i.e. forests, scrublands, and grasslands in high altitudes/ at higher elevations; while croplands and orchards occupy 31% (CREAF, 2009). The main tree genera are *Pinus* (e.g. *P. halepensis*, *P. nigra*, *P. pinea*, *P. sylvestris*, *P. pinaster*) and *Quercus* (e.g. *Q. suber*, *Q. ilex*, *Q. faginea*, *Q. humilis*), complemented by forests of *Fagus sylvatica*, *Abies alba*, and other less well represented species (Figure C.1). Most of the species have co-evolved with fires, developing fire-resistant and/or fire-adaptive strategies such as the ability to resprout (e.g. oak species), develop serotinous cones (e.g. *P. halepensis*), and/or to produce a thick protective bark (e.g. *P. pinaster*). They have also developed adaptations to cope with a severe water deficit during the summer seasons. However, predicted climate warming along with an increase in fire occurrence and severity for these fire-prone systems can compromise species resilience to both fires and drought (Díaz-Delgado *et al.*, 2002; Espelta *et al.*, 2008).

Forests and scrublands have increased in abundance at the expense of agricultural lands during the last five decades. A widespread economic and social transition from a rural-based to an industrial-/urban-based model has triggered a rapid and significant rural abandonment process. In only 16 years, from 1993 to 2009, ca. 1 600 km^2 (that is 100 $km^2 \cdot year^{-1}$) of mainly agricultural lands has been transformed into semi-natural forests (Table C.1). Urbanization is responsible for 2.1% of land change in that period (Table C.1). Catalonia currently has a population of over 7.5 million, resulting in a 33% population increase in the last 40 years (IDESCAT, 2016). Human population is mostly concentrated around the Barcelona hub, but distributed along the coast and a few transportation-communication axes (Figure C.1). However, the economic-territorial model has encouraged families to move to (or to have a second residence in) the urban-wildland interface, where houses are literally embedded in the forest. Such interfaces are very sensitive to fires because of the proximity to semi-natural lands with a high fuel load and a dense secondary road network that favours recreation activities that are known to increase fire ignition events (Badia *et al.*, 2011; González-Olabarria *et al.*, 2012). In Catalonia, most of the ignitions are human-caused, either intentional or accidental.

During the last 36 years, 10.1% of the territory burned in fires of $\geq$ 50 ha (GENCAT, 2016); whereas between 1975 and 1998, ca. 13% of land burned at least once (Díaz-Delgado *et al.*, 2004) (Figure C.2). Fire suppression, with specialized forest fire fighter brigades, has been the main strategy for reducing fire impacts on Catalonia, and in general on all Mediterranean landscapes. Even so, some fires regularly burn out of control every season, endangering human infrastructure, human life and valuable forest ecosystems. Experts and scientists are advocating for a new fire prevention strategy – a fire suppression model is needed not only for Catalonia, but for all the Mediterranean area, as global change factors are increasing fire risk in these areas.

Table C.1: Area (in km^2) changed under each land transition in Catalonia during the reference period according to the Land Cover Map of Catalonia (versions 1 and 4), and the equivalent area changed in 1-year and 5-year time spans. The base amount used to set the annual agricultural conversion demand in our factorial design is shown in bold print.

Demand for:	**1993 to 2009**	**1 year**	**5 years**
Urbanization	690	43	216
Rural abandonment	1599	100	500
Agricultural conversion	355	22	111

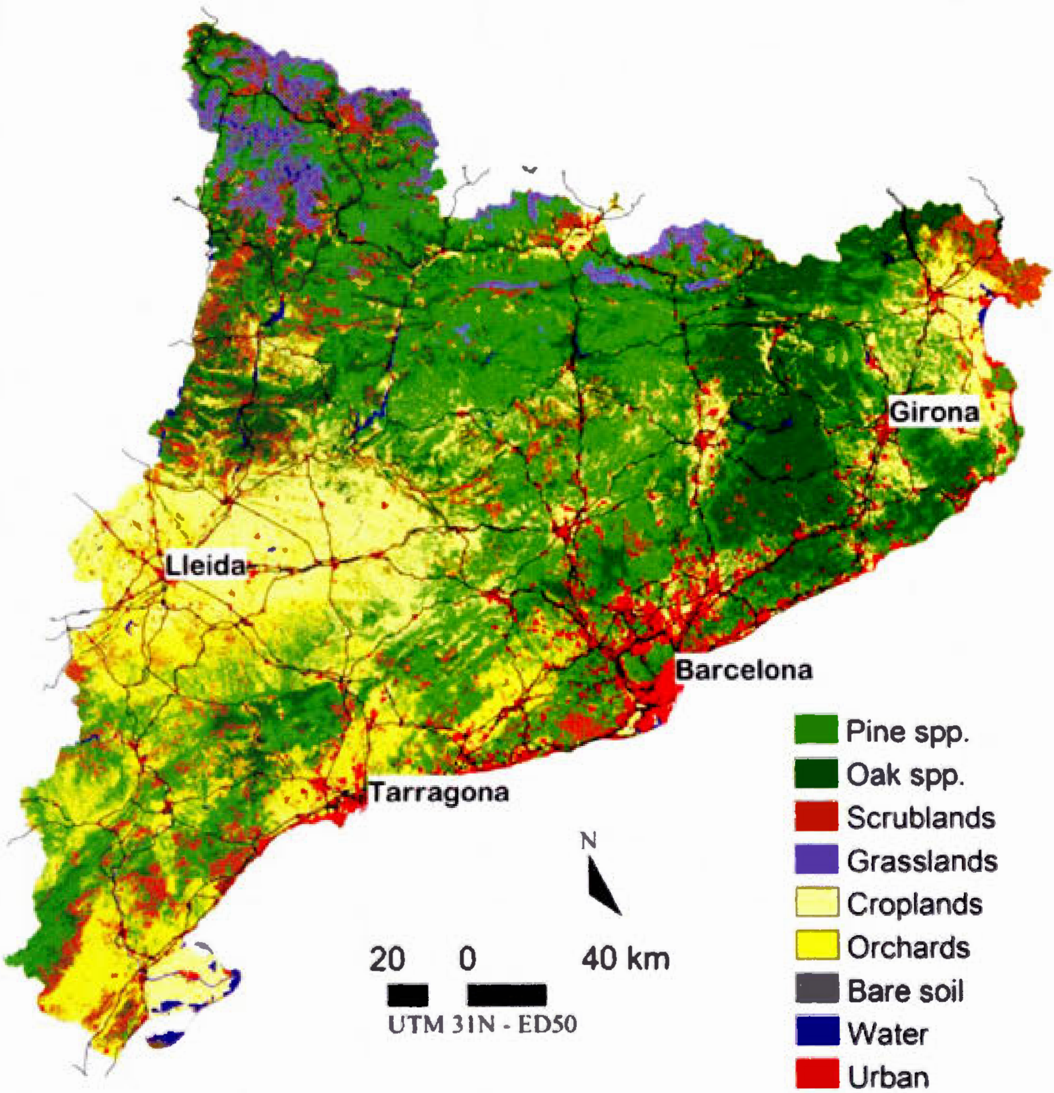

Figure C.1: 2010 Land-cover and forest species map, with the main roads and highways, and the four provincial capitals.

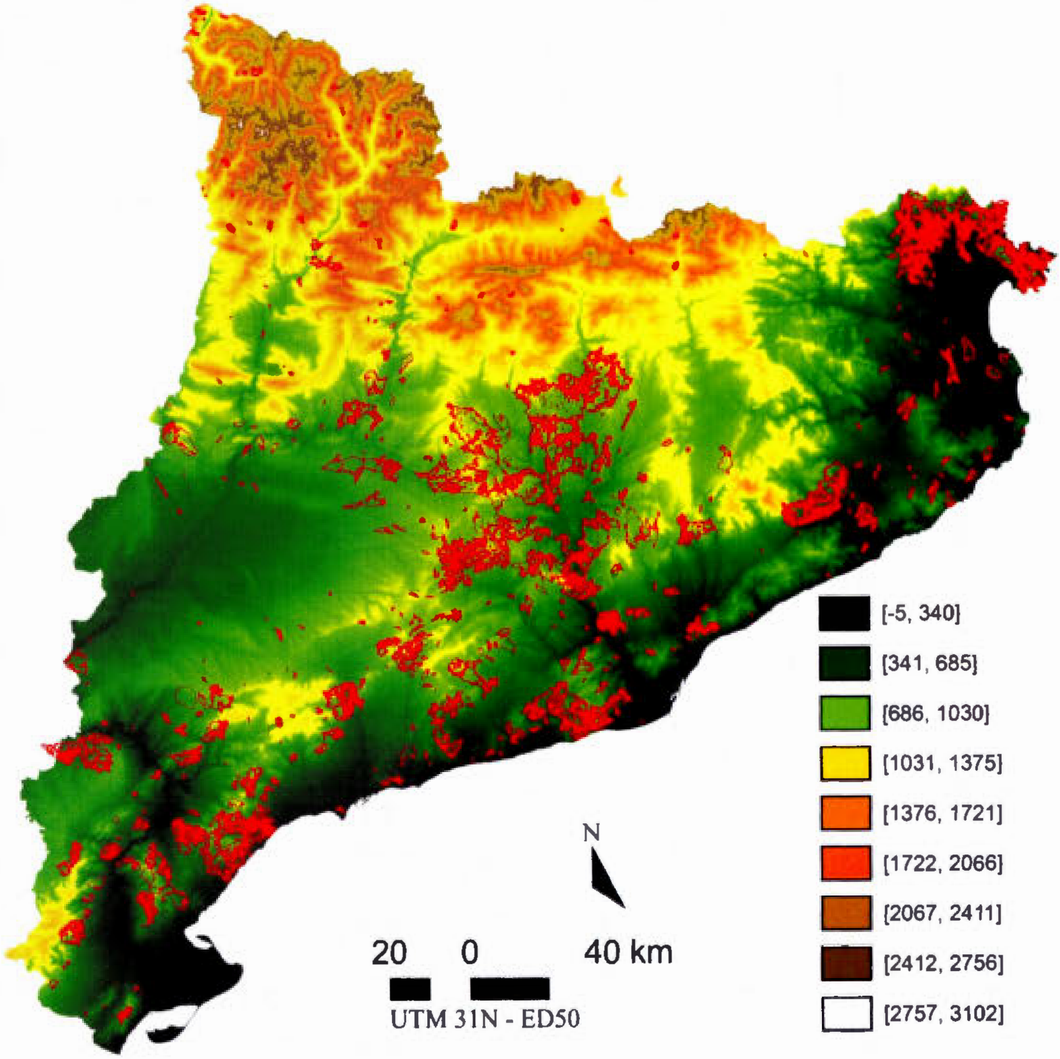

Figure C.2: Digital elevation map of Catalonia (range of [-5, 3102]) and fire perimeters (≥ 50 ha) for 1980 – 2015 in red.

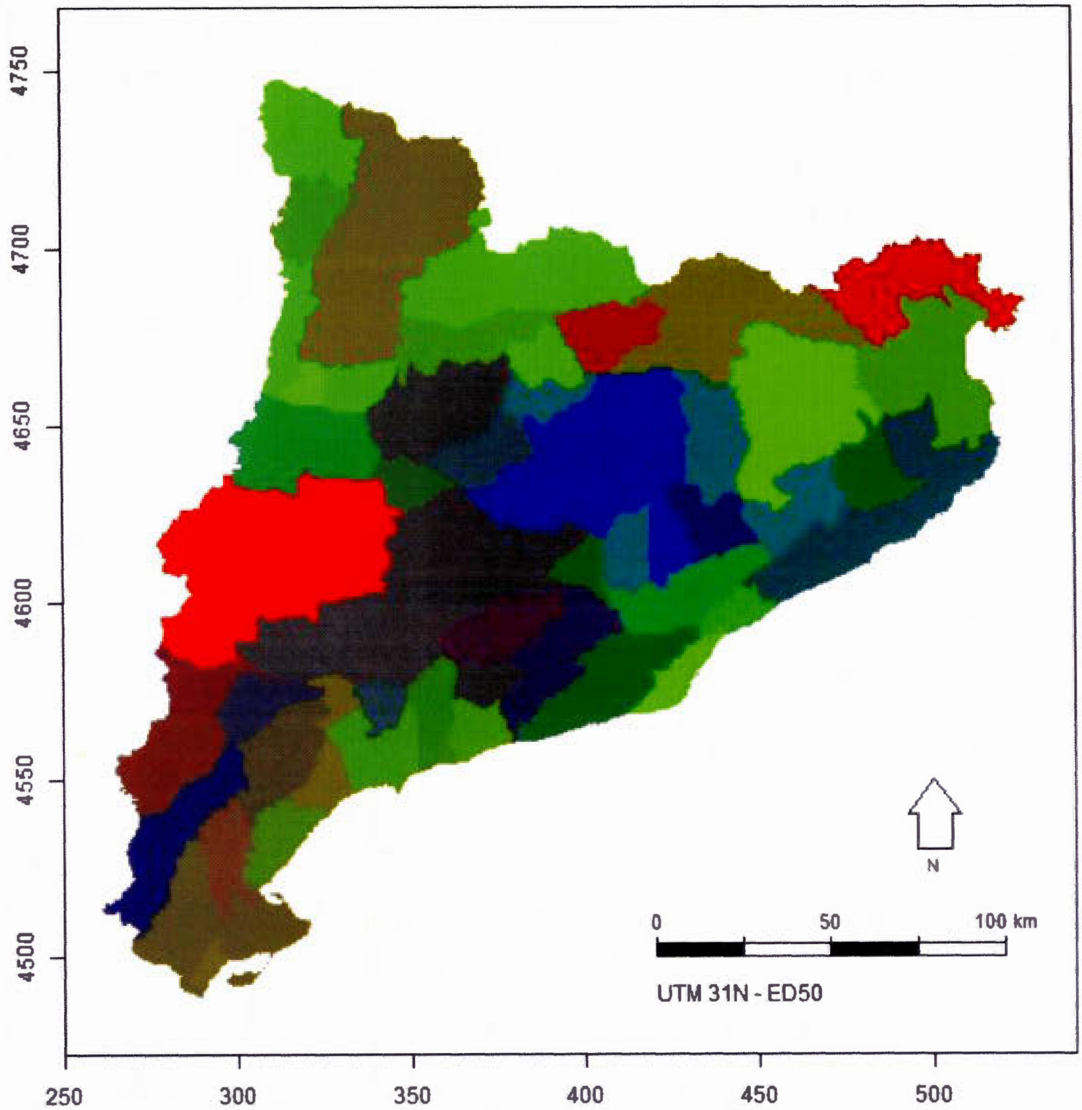

Figure C.3: 72 homogeneous fire regime zones of Catalonia. Each zone is characterized by the predominant percentage of wind-driven, topographic-driven and convective fire spread types. Colours in the map are proportional RGB combination of wind-driven (red), topographic-driven (green), and convective (blue) fire spread types. Units on the *x*-axis and *y*-axis are in km.

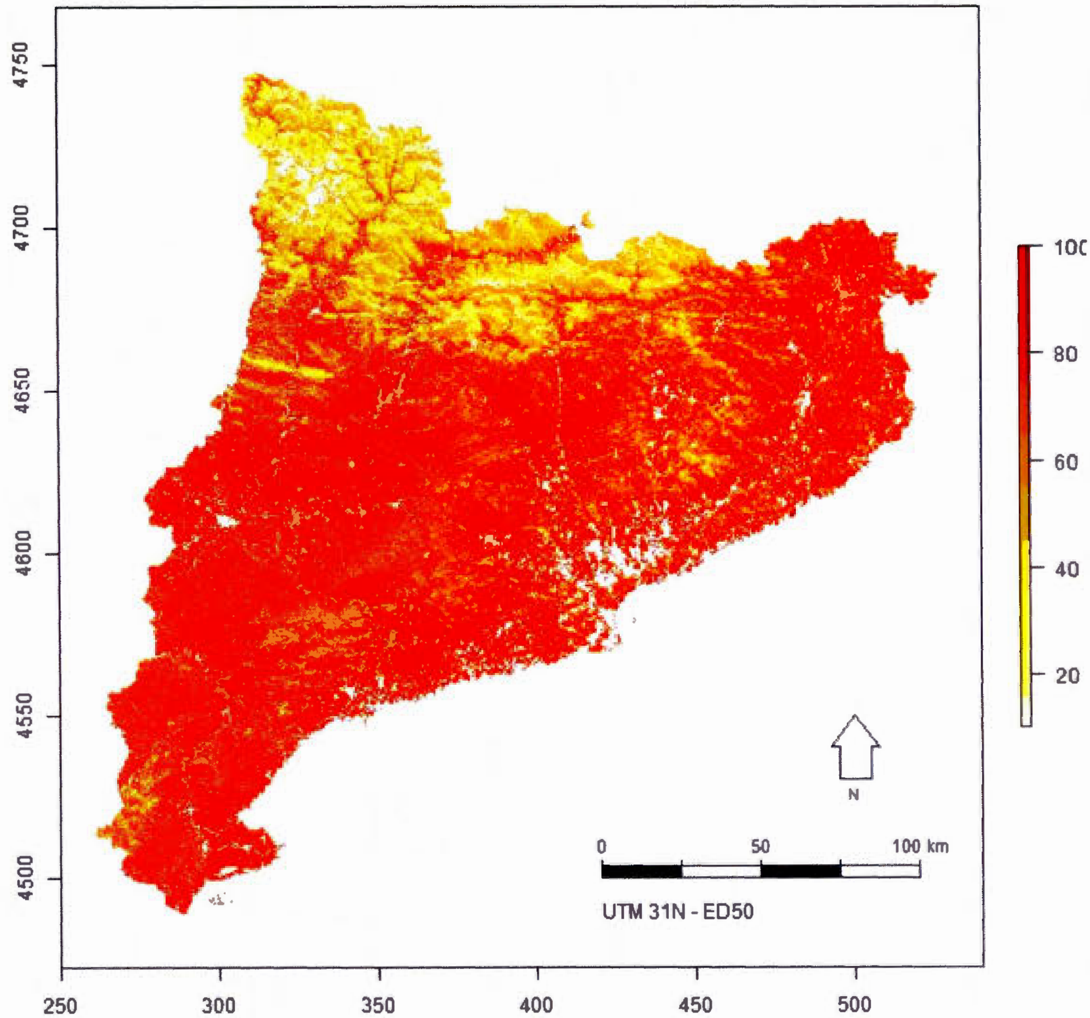

Figure C.4: Orographic fire risk (10 classes). Units on the *x*-axis and *y*-axis are in km.

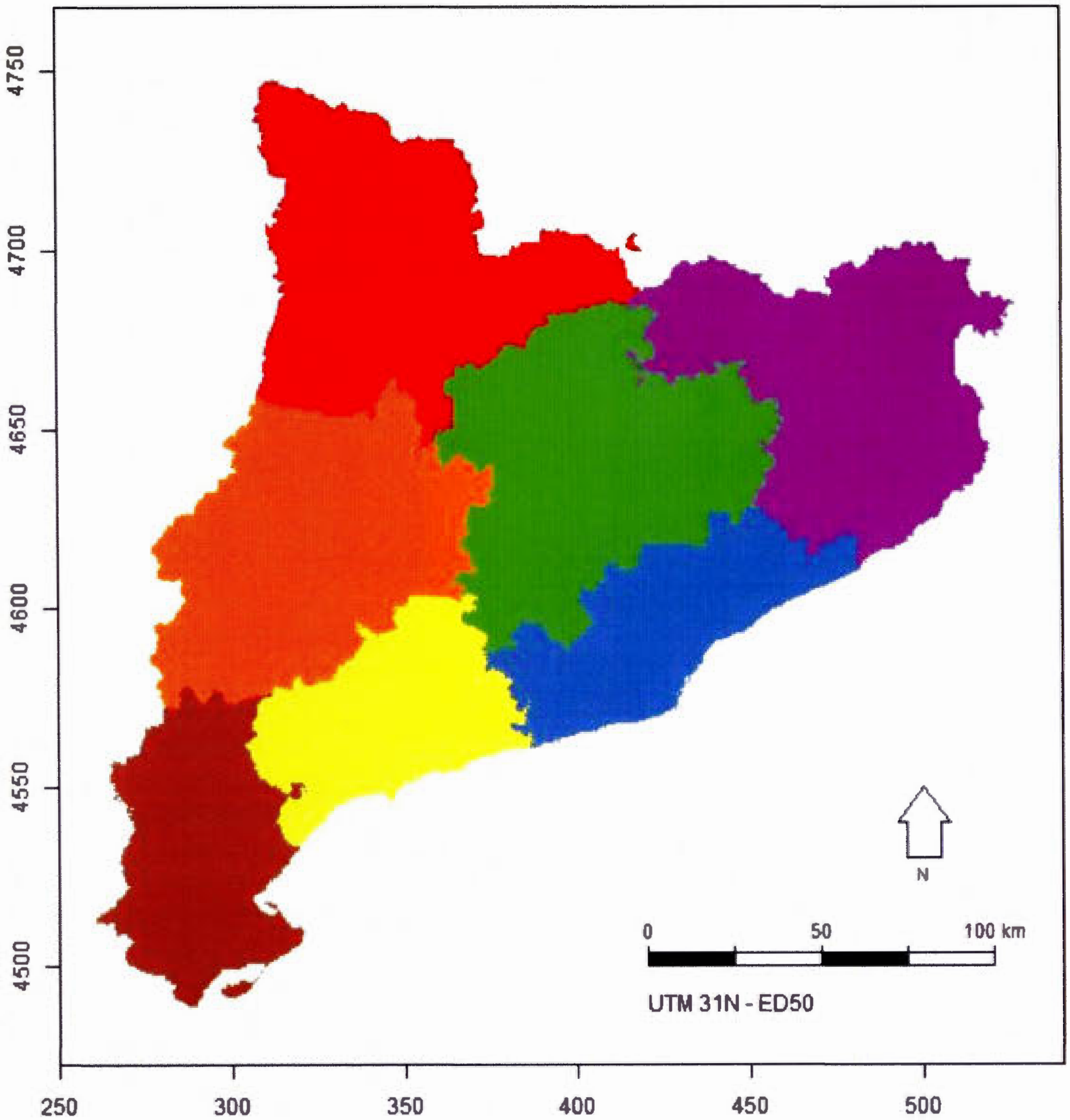

Figure C.5: Seven *vegueries* of Catalonia (administrative - biogeographical division). Units on the x-axis and y-axis are in km.

ANNEX D

INITIALIZATION OF MEDFIRE AND MEDLUC MODELS - CHAPTER 2

D.1 Landscape composition of Catalonia

Landscape composition influences landscape level processes that are key to our system, such as the probability of fire ignition (González-Olabarria *et al.*, 2012) and the land-cover transitions (Aquilué *et al.*, 2017). For fire ignition risk and land transitions the interplay between human presence on the territory and natural areas is relevant. In the current application of the meta-model, the land-cover / forest species state variable describes (at the finer spatial and thematic resolutions) the landscape composition of the study area. It is a categorical layer at 1 ha consisting of 19 classes: 12 tree species, 2 semi-natural land (scrublands and grasslands), 2 agricultural land (croplands and orchards), and 3 non-productive land (urban, bare soil, and water). But to better capture the landscape mosaic at the neighborhood level we defined seven interfaces or mixed categories at 1 km^2 (Table D.1, Figure D.1) following González-Olabarria *et al.*, (2011). Three of these interfaces combine different land-cover types. The wildland-urban interface are zones where homes meet natural areas, the agro-urban interface are zones where urban areas meet agricultural land, and the agro-forestry interface is where semi-natural and natural areas mix with croplands and pastures. To integrate the interface factor with both the probability of fire ignition and the potential-transition of each land-cover change process, we adopted the neighborhood factor introduced by Verburg *et al.*, (2004). The neighborhood factor quantifies the presence or degree of influence of each interface at the cell level. It is computed as the proportional amount of an interface within a square neighborhood of size r (= 3 km) around each cell, weighted by the importance of the interface in the landscape.

Table D.1: Rules of reclassification of the state variable land-cover / forest species to derive seven broad interface categories. Because the rules are not exclusive, some cells of the original map (41 %) were not classified in the first step. The rules were then relaxed, so 1 km^2 cells with a majority presence ≥ 75 % 80%? were assigned to one of the *Urb*, *Crp*, *Nat*, or *Oth* categories. Finally, cells characterized as Urban < 20 % and Agriculture ≥ 15 % and (Forest + Scrubland + Grassland) ≥ 15 %, or (Agriculture + Forest + Scrubland + Grassland) ≥ 75 % were classified as *CrpNat*.

ID	Interface	Rule
1	*Urb*	Urban ≥ 80 %
2	*Crp*	Agriculture ≥ 80 %
3	*Nat*	Forest + Scrubland + Grassland ≥ 80 %
4	*Oth*	Bare soil & Water ≥ 80 %
5	*UrbCrp*	Urban ≥ 20 % & Agriculture > 30 %
6	*UrbNat*	Urban ≥ 20 % & (Forest + Scrubland + Grassland) > 30 %
7	*CrpNat*	Urban < 20 % & Agriculture ≥ 20 % & (Forest + Scrubland + Grassland) ≥ 20 %

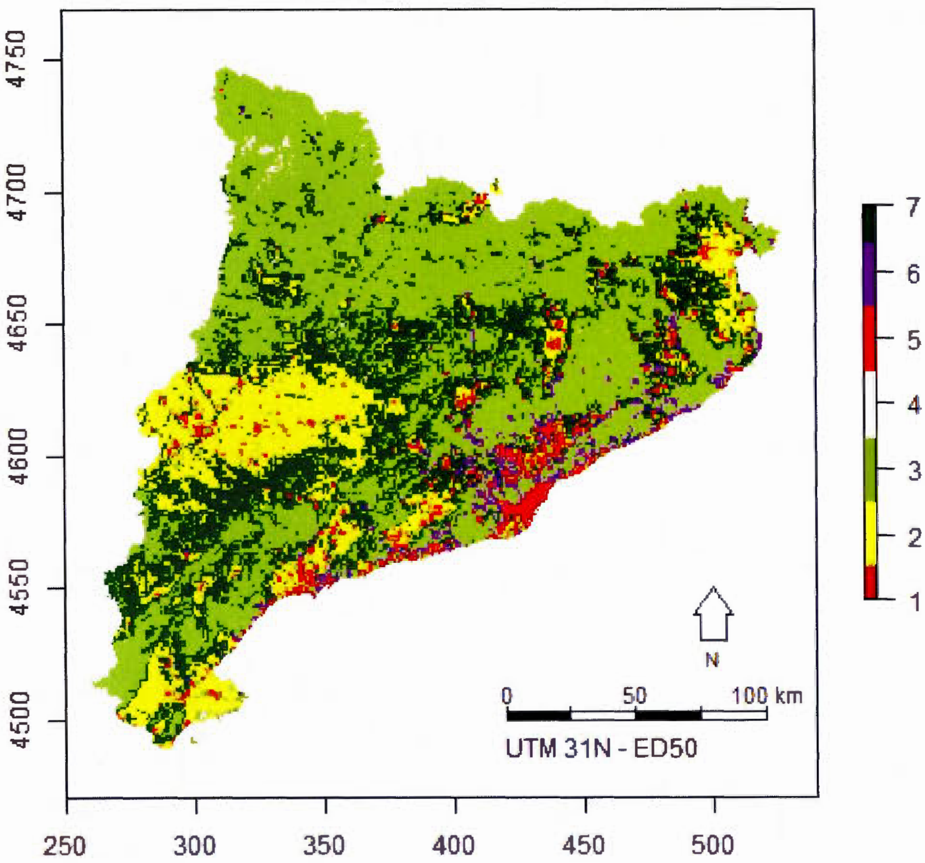

Figure D.1: Initial interfaces map derived from the 2010 land-cover / forest species map of Catalonia (Figure C.1). Legend is for interfaces ID listed in Table D.1. Units on the x-axis and y-axis are in km.

D.2 The fire regime in the MEDFIRE model

The MEDFIRE model applies a top-down fire regime defined by annual target areas and fire sizes. We compiled climatic data and fire statistics for the 1980 - 2010 period to empirically characterize the fire regime of Catalonia. Firstly, we classified as climatically adverse those years with a value of the cumulative soil water deficit (CSWD) index above 270 mm (Gil-Tena *et al.*, 2016). CSWD is the average between the cumulative soil water deficit of the current and preceding years calculated following a Thornthwaite-type approach. Secondly, for each subset of years (normal vs. severe) we used fire stats to fit both annual burnt area distribution by a lognormal, and both fire size distributions by a power law (Brotons *et al.*, 2013) (Table D.2). In the current application of MEDFIRE, as the annual burnt area of the first five years (from 2011 to 2015) was known, the model effectively burned the observed areas.

Table D.2: Parameters of the lognormal and power law distributions modeling annual burnt area and fire size distributions for Catalonia, respectively.

Climatic severity	**Annual target area**		**Fire size**	
	μ	**σ**	**α**	**β**
Normal	7.81	1.40	3.63	0.78
Severe	8.74	1.39	3.60	0.71

D.3 Probability of fire ignition

The probability of ignition accounts for climatic, biogeographic, and human-driven factors and is dynamic as long as landscape configuration (due to land-cover changes) or climate vary over time (Equation D.1). We calibrated the probability for a previous study in the Catalan region (Gil-Tena *et al.*, 2016) using fire ignition data from a 24-year time span, representative climatic data, and the 1993 and 2007 versions of the Land Cover Map of Catalonia (http://www.creaf.uab.es/mcsc).

$$\text{logit (Ignition | non-Ignition)} = 6.5 - 0.28\cdot Temp - 0.0099\cdot Precip + 0.00035\cdot Highw + 0.00020\cdot Road + 0.00054\cdot Rail + 0.58\cdot Nat + 2.95\cdot UrbNat + 2.73\cdot CrpNat + 0.099\cdot Temp \times Nat \qquad \text{[D.1]}$$

where *Temp*: mean maximum summer temperature (in °C); *Precip*: mean accumulated spring and summer precipitation (in mm); *Highw*: density of highways (km/km2); *Road*: density of secondary roads (km/km^2); *Rail*: density of railways (km/km2); *Nat*, *UrbCrp*, *UrbNat*, and *CrpNat* are Boolean variables indicating the presence of the respective interfaces as indicated above (Table D.1, Figure D.1).

D.4 Fire spread rate

Spread rate (*SR*) (Equation D.2) is calculated for its 8 neighbors following a polynomial model where explanatory factors are species flammability (*SppFlam*) (Table D.3), fuel load (*Fuel*), aspect (*Aspect*), slope in relation to fire front (*Slope*), and wind effect in relation to dominant wind direction (*Wind*). These explanatory variables are multiplied by weight-parameters (*wSpp*, *wF*, *wA*, *wS*, and *wW* ; Table

D.4) representing the relative influence of each factor on fire front progression (Duane *et al.*, 2016):

$$SR = wW \cdot Wind + wS \cdot Slope + wA \cdot Aspect + wF \cdot Fuel + wSpp \cdot SppFlam \qquad [D.2]$$

Table D.3: Flammability of land-cover types and tree species for each of the three fire spread patterns: wind-driven, topographic-driven, and convective.

	Wind-driven	Topographic-driven	Convective
Pine	0.50	0.60	0.60
Oak	0.45	0.50	0.50
Other trees	0.40	0.40	0.40
Scrubland	0.90	0.90	0.70
Alpine grass	0.10	0.10	0.10
Agriculture	0.15	0.15	0.15

Table D.4: Weights of the five explanatory factors for spread rate according to the three fire spread patterns: wind-driven, topographic-driven, and convective.

Factor	**Wind-driven**	**Topographic-driven**	**Convective**
Wind	0.43	0.09	0.15
Slope	0.33	0.53	0.38
Fuel	0.00	0.00	0.00
SppFlam	0.21	0.39	0.48
Aspc	0.04	0.00	0.00

D.5 Afforestation

The annual probability of afforestation (Equation D.3) is a function of the number of forest ≥ 15 years in a 150 m radius (*ForNeigh*), mean maximum summer temperature (*Temp*), mean accumulated spring and summer precipitation (*Precip*), potential summer solar radiation (*RadSol*), slope (*Slope*), and scrubland age (TSF_{shrub}) (Gil-Tena *et al.*, 2016). Only tree species over their maturity age within a 2 km circular neighbourhood are potential colonizers. A tree species is proportionally selected from this pool of species, whit conifers having twice the colonization power compared to oaks and other deciduous species.

$$logit\ (P_{afforestation|non\text{-}afforestation}) = -11.62 + 2.951 \cdot ForNeigh - 0.9559 \cdot ForNeigh\hat{}2 + 0.081 \cdot Temp - 0.00013 \cdot Temp\hat{}2 + 0.0015 \cdot Precip - 0.000000068 \cdot Precip\hat{}2 - 0.033 \cdot Slope + 0.00035 \cdot Slope\hat{}2 - 0.0039 \cdot RadSol + 0.00000074 \cdot RadSol\hat{}2 + 0.37 \cdot TSF_{shrub} - 0.011 \cdot TSF_{shrub}\hat{}2 - 0.0000033 \cdot Temp \times Precip \qquad [D.3]$$

D.6 The spatial contagion of changes in MEDLUC model

The MEDLUC land-use/land-cover (LULC) change model relies on a demand-allocation approach to simulate LULC transitions, meaning that the amount of land claimed by each transition (i.e. the demand) is an input, while the spatialization of the demand is determined during the allocation procedure inherent in MEDLUC. In this modeling framework, the user defines each land transition as to the land-use/land-covers that potentially could change to the target land-cover. The spatial allocation procedure is general and flexible enough to simulate any land transition and replicate empirical processes of change observed in Catalonia, such as urbanization, rural abandonment, and agricultural conversion (Aquilué *et al.*, 2017). It consists of four basic steps for each LULC transition: (1) the number of cells are randomly selected according to a transition-potential map, (2) a processing time T_{ini} following an exponential distribution of rate λ_i is assigned to each initiation cell ($T_{ini} \sim$ NEGEXP(λ_i)); these cells are sorted in ascending-order according to T_{ini} values, (3) the first cell in the queue undergoes change, and (4) a processing time as $T_{sprd} \sim$ NEGEXP(λ_s) $\times$ $(T_{ini})^k + T_{src}$ is computed for the 4 neighbors; these cells are then returned to the ascending-order queue. Steps (3) and (4) are sequentially repeated until all demand is allocated and non-processed cells in the queue are discarded. The rate of change-occurrence λ_i determines the relative speed at which patches-of-change are created, the rate of change-contagion λ_s indicates the speed at which land change spatially spreads, while k controls the acceleration of this induced change.

The allocation procedure was calibrated to reproduce the empirical patches-of-change size distributions (at 1 ha of spatial resolution) extracted for Catalonia in a 16-year period (Aquilué *et al.*, 2017). The maximum likelihood parameter combinations $\{\lambda_i, \lambda_s, k\}$ for urbanization, rural abandonment, and agricultural conversion transitions were {10, 0.5, 0.5}, {1, 0.05, 0.5}, and {2.5, 0.1, 0.3} respectively. In the present study, urbanization transition was allocated based on the observed patterns, while agriculture conversion was allocated following two extreme patterns (Figure D.2): an aggregate one was generated by the combination {0.25, 10, 0.3} and a scattered one by {2.5, 0.1, 0.3}.

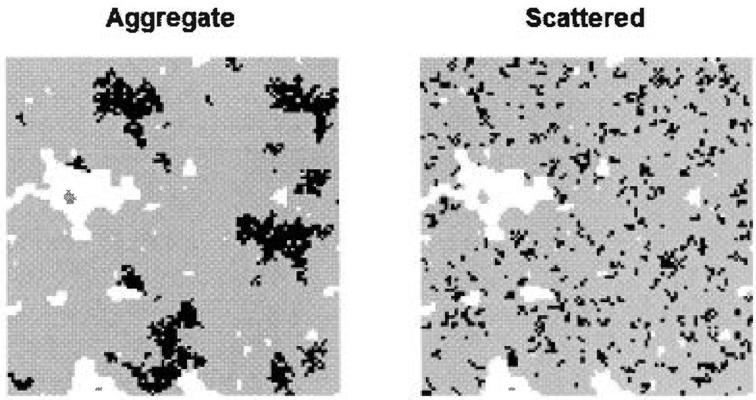

Figure D.2: Representation of the two spatial patterns (i.e. aggregate and scattered) adopted to allocate agricultural land in the landscape. New agricultural land (black patches) represents 10% of this neutral landscape, white areas cannot convert to agricultural land. Spatial extent is 100×100 cells.

D.7 Transition-potential maps

A transition-potential map describes where is more likely a LULC change occur. The transition-potential maps used to allocate new croplands in the Fire Management, Rural Development, and Crop Productivity strategy are derived from Equation D.4, Equation D.5, and Equation D.6 respectively.

$$TPOT_{FM} = (0.5 \cdot FireRisk + 0.25 \cdot NF\_UrbNat + 0.25 \cdot NF\_CrpNat) \cdot Mask \quad [D.4]$$

$$TPOT_{RD} = (0.5 \cdot 100 \,/\, SlopePctg + 0.5 \cdot NF\_Nat\,) \cdot Mask \quad [D.5]$$

$$TPOT_{CR} = (0.2 \cdot 100 \,/\, SlopePctg + 0.4 \cdot NF\_Crp + 0.4 \cdot NF\_UrbCrp) \cdot Mask \quad [D.6]$$

In Equation D.4, the spatial variable *FireRisk* is a categorical classification of the static fire risk based on orographic features (Figure C.4). The *SlopePctg* variable is the slope in % of the terrain. The *NF_Crp*, *NF_Nat*, *NF_CrpNat*, *NF_UrbCrp*, and *NF_UrbNat* are the neighbour factors of agricultural, natural, agro-forest, agro-urban, and wildland-urban interfaces respectively (see the first section). Interfaces are aggregations of land-cover types at a coarser scale (1 km^2) better describing the landscape mosaic. The neighbour factor of an interface, measured in a neighbourhood of size r indicates the influence of that land-cover within the neighbourhood inversely proportional to its presence on the landscape (Verburg *et al.*, 2004). Here, it is calculated in a squared neighbourhood of size r = 3 km. We restricted new croplands to relative low altitudes (≤ 1250 m, that is the 99^{th} percentile of current croplands elevation) and relative young forest (≤ 97 years, that is the 90^{th} percentile of forest age distribution). *Mask* is simply equal to (*Elevation* ≤ 1250) and (*Forest Age* ≤ 97).

ANNEX E

COMPLEMENTARY RESULTS - CHAPTER 2

E.1 Fire suppression effectiveness and effects of agriculture conversion on mean forest patch core area

To determine whether an agricultural conversion scenario performed better than the control scenario (in which no conversion took place), we compared the fire suppression effectiveness of each scenario during the 40-year period with the effectiveness of the control scenario. Because each scenario was simulated 30 times, we used a Mann-Whitney-Wilcoxon test to compare the effectiveness distribution of any pair of scenarios (Table E.1). We used this non-parametric test because 8 out of 25 scenarios were not normally distributed.

Table E.1: Statistic and *p*-value of the Mann-Whitney-Wilcoxon test when comparing the effectiveness of each agricultural conversion scenario and the effectiveness of the control scenario (no conversion). The null hypothesis is that the two distributions are identical populations. Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1.

Scenario	***W***	***p*-value**	
CP_D2_AGG	507	4.06E-01	
CP_D2_SPR	401	4.76E-01	
FM_D2_AGG	513	3.58E-01	
FM_D2_SPR	428	7.52E-01	
RD_D2_AGG	570	7.72E-02	.
RD_D2_SPR	404	5.04E-01	
CP_D_AGG	640	4.53E-03	**
CP_D_SPR	536	2.08E-01	
FM_D_AGG	644	3.72E-03	**
FM_D_SPR	638	4.99E-03	**
RD_D_AGG	637	5.24E-03	**
RD_D_SPR	595	3.19E-02	*
CP_2D_AGG	811	5.87E-09	***
CP_2D_SPR	743	5.76E-06	***
FM_2D_AGG	848	3.02E-11	***
FM_2D_SPR	797	3.06E-08	***
RD_2D_AGG	835	2.31E-10	***
RD_2D_SPR	835	2.31E-10	***
CP_3D_AGG	879	5.93E-14	***
CP_3D_SPR	847	3.57E-11	***
FM_3D_AGG	880	4.59E-14	***
FM_3D_SPR	869	6.00E-13	***
RD_3D_AGG	872	3.12E-13	***
RD_3D_SPR	883	2.05E-14	***

Table E.2: Mean fire suppression effectiveness of the 40-year period for each scenario (μE_1), and aggregated at the demand level (μE_6); and mean leverage of the 40-year period for each scenario (μL_1) and aggregated at the demand level (μL_6).

Scenario	μE_1	μE_6	μL_1	μL_6
CP_D2_AGG	0.13	0.11	0.28	0.26
CP_D2_SPR	0.10		0.24	
FM_D2_AGG	0.12		0.30	
FM_D2_SPR	0.11		0.25	
RD_D2_AGG	0.12		0.26	
RD_D2_SPR	0.10		0.23	
CP_D_AGG	0.14	0.14	0.16	0.16
CP_D_SPR	0.13		0.15	
FM_D_AGG	0.15		0.16	
FM_D_SPR	0.15		0.19	
RD_D_AGG	0.15		0.17	
RD_D_SPR	0.12		0.14	
CP_2D_AGG	0.23	0.21	0.13	0.12
CP_2D_SPR	0.22		0.12	
FM_2D_AGG	0.24		0.15	
FM_2D_SPR	0.20		0.11	
RD_2D_AGG	0.21		0.13	
RD_2D_SPR	0.17		0.10	
CP_3D_AGG	0.28	0.27	0.10	0.11
CP_3D_SPR	0.29		0.11	
FM_3D_AGG	0.29		0.13	
FM_3D_SPR	0.26		0.10	
RD_3D_AGG	0.28		0.12	
RD_3D_SPR	0.25		0.10	
URB	0.11		-	

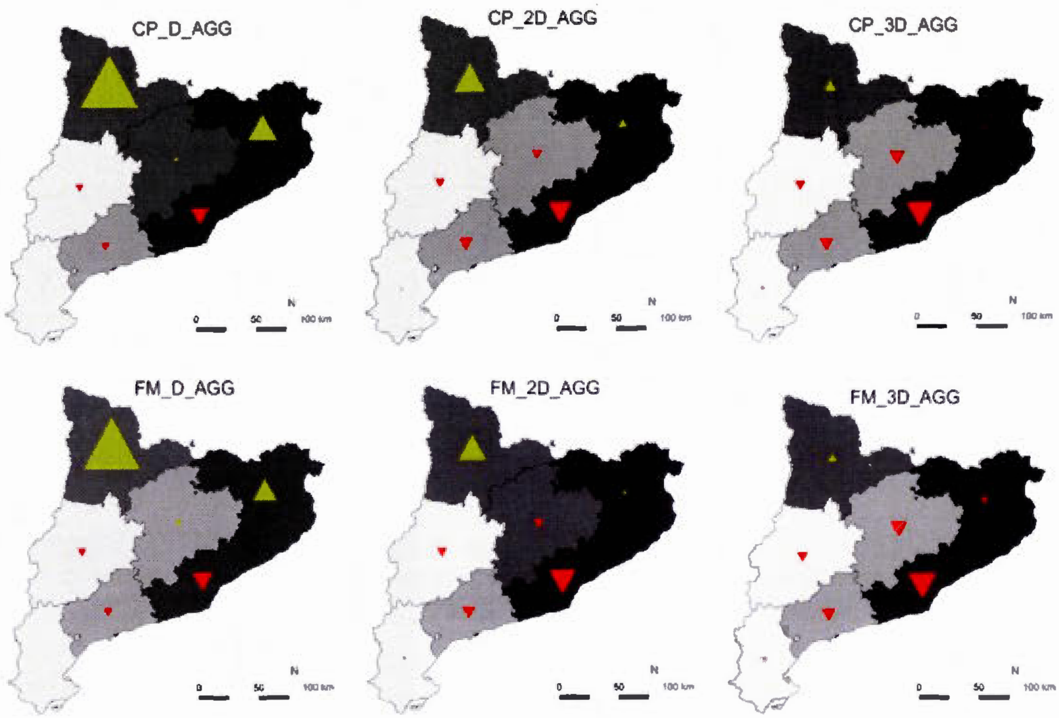

Figure E.1: Proportional increase (triangles that point upwards) or decrease (triangles that point downwards) of the forest patches mean core area in the 7 *vegueries* for the scenarios allocating new agricultural land aggregately (AGG), under the storylines crop productivity (CP) and fire management (FM), and for the rate conversion rates of D = 100 $km^2 \cdot year^{-1}$, 2D = 200 $km^2 \cdot year^{-1}$, and 3D = 300 $km^2 \cdot year^{-1}$. Grey background accounts for the standard deviation of the metric (that increases as grey becomes darker).

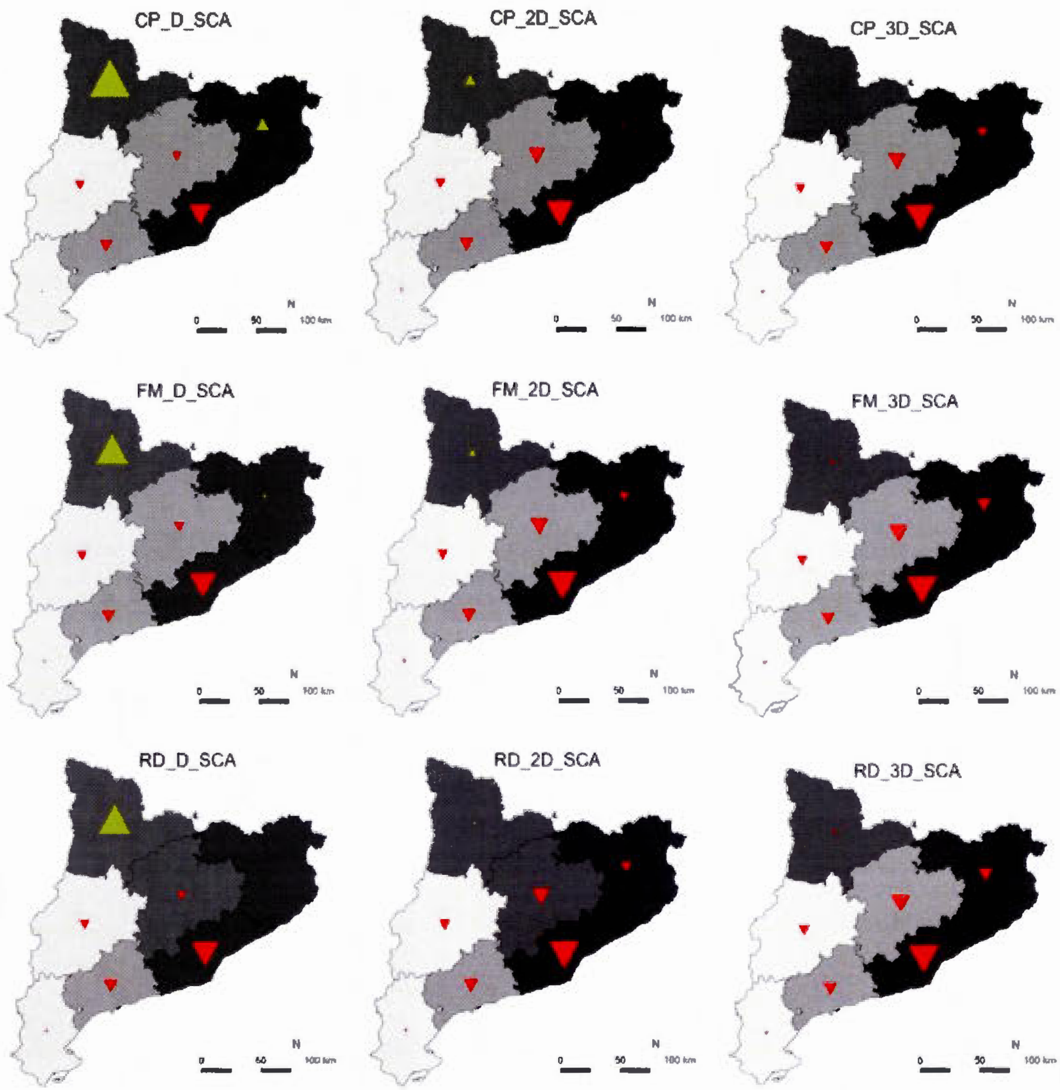

Figure E.2: Proportional increase (triangles that point upwards) or decrease (triangles that point downwards) of the forest patches mean core area in the 7 *vegueries* for the scenarios allocating new agricultural land scattered (SCA), under the storylines crop productivity (CP), fire management (FM), and rural development (RD), and for the rate conversion rates of D = 100 $km^2 \cdot year^{-1}$, 2D = 200 $km^2 \cdot year^{-1}$, and 3D = 300 $km^2 \cdot year^{-1}$. Grey background accounts for the standard deviation of the metric (that increases as grey becomes darker).

E.2 Land available for agriculture conversion and evolution of transition-potential maps

As agricultural expansion takes place in landscapes, less natural and semi-natural land is available for the allocation of new croplands (Figure E.3). The initial percentage of land available for conversion to agricultural land is dictated by the amount of area covered by vegetation at altitudes $\leq$ 1250 m verifying that forest age $\leq$ 97 years old. The spatial distribution of land available to undergo change varies by strategy as allocation of agricultural area is driven by different factors (Figure 2.3, Annex D). Likewise, the transition-potential is a dynamic variable that evolves as time goes on (and available land is converted to agricultural land) depending on the spatial distribution of land-cover types at each time step (Figures E.4 and E.5). Both spatial distributions depend on the amount of new agricultural land (i.e. the demand) and the allocating spatial pattern.

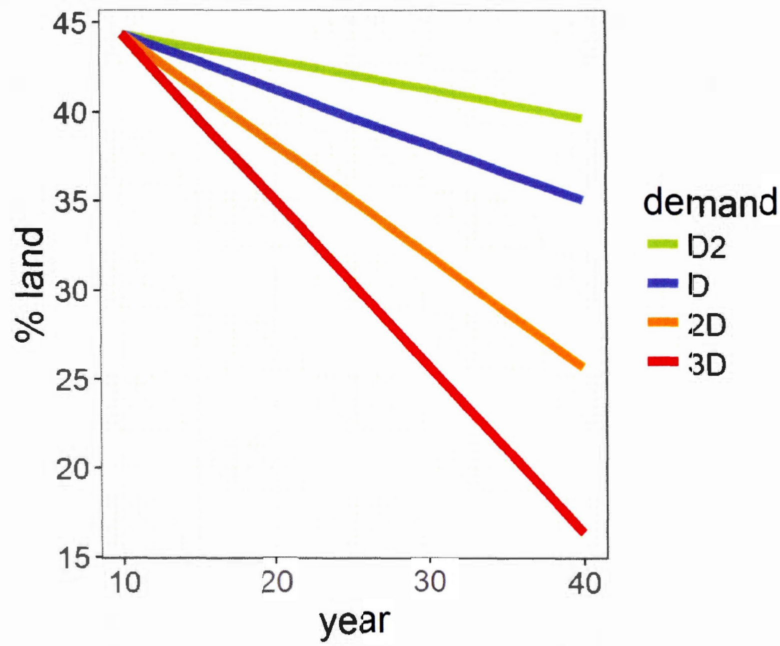

Figure E.3: Evolution of available percentage of land to undergo the transition to agricultural land according to the demand (D2 = 50 $km^2 \cdot year^{-1}$, D = 100 $km^2 \cdot year^{-1}$, 2D = 200 $km^2 \cdot year^{-1}$, and 3D = 300 $km^2 \cdot year^{-1}$) allocated every 5 years over 40 years.

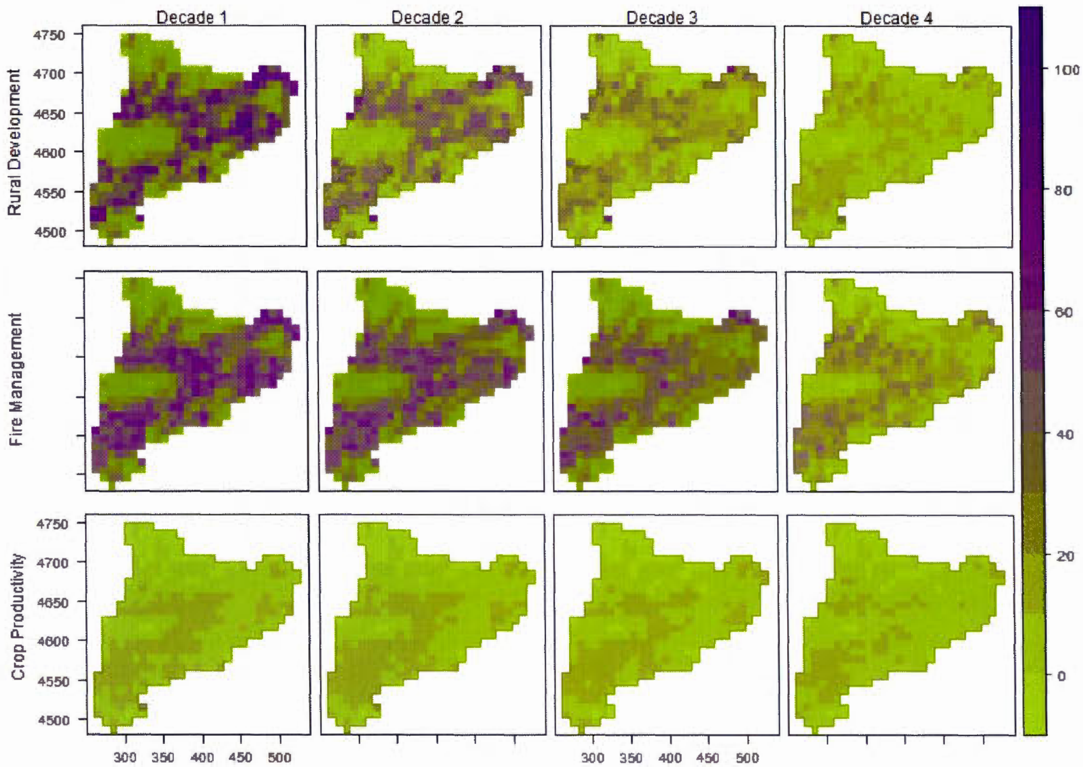

Figure E.4: Percentage of land available for conversion to agriculture every decade (over four decades) when the rate of land conversion is 200 $km^2 \cdot year^{-1}$ and the spatial pattern of new patches is aggregated. Each row of maps is a different strategy. Spatial resolution is 10 km^2.

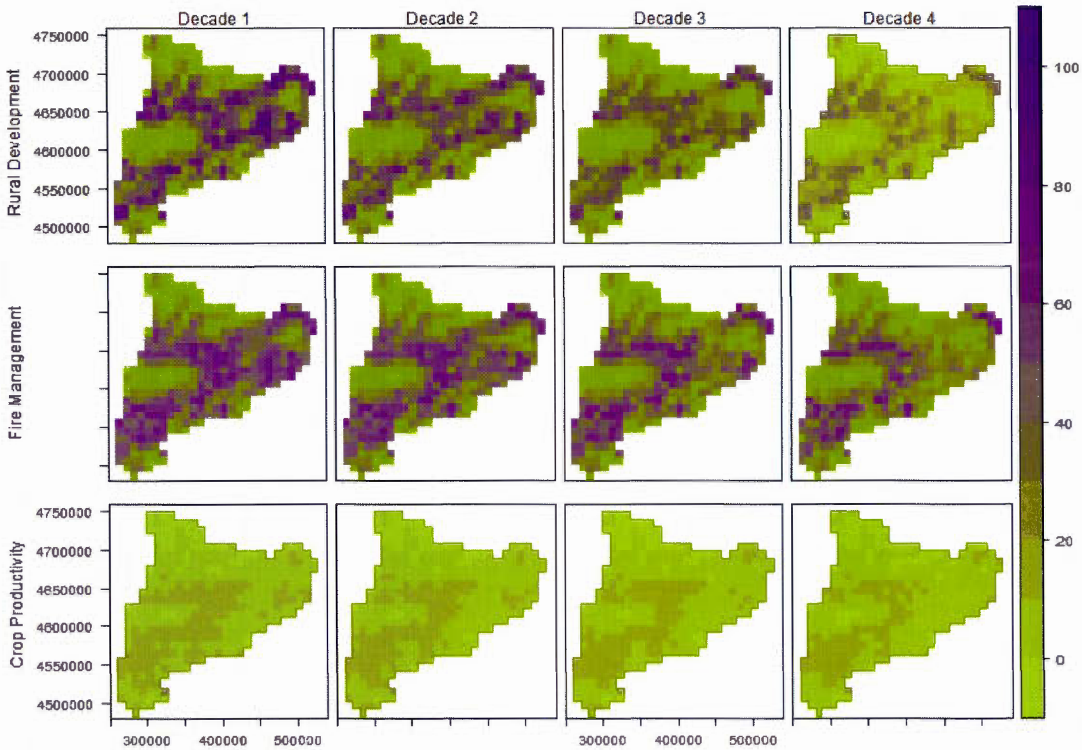

Figure E.5: Transition potential map for agricultural expansion every decade (over four decades) when the rate of land conversion is 200 $km^2 \cdot year^{-1}$ and the spatial pattern of new patches is scattered. Each row of maps is a different strategy. Spatial resolution is 10 km^2.

ANNEX F

ADDITIONAL DETAILS OF METHODS - CHAPTER 3

Table F.1: Tree species identified in 42 sites of the Central Québec region, their relative abundance and the estimated dispersal distance capacity (in m).

SppCode	Family	Genus	Species	Type	Relative Abundance	Dispersal Distance
BET_AL	Betulaceae	Betula	alleghaniensis	deciduous	4.05	250
BET_PA	Betulaceae	Betula	papyrifera	deciduous	1.32	475
BET_PO	Betulaceae	Betula	populifolia	deciduous	5.63	64
OST_VI	Betulaceae	Ostrya	virginiana	deciduous	0.10	226
THU_OC	Cupressaceae	Thuja	occidentalis	deciduous	3.17	942
FAG_GR	Fagaceae	Fagus	grandifolia	deciduous	0.68	4000
JUG_CI	Juglandaceae	Juglans	cinerea	deciduous	0.04	763

TIL_AM	Malvaceae	Tilia	americana	deciduous	0.07	1300
FRA_AM	Oleaceae	Fraxinus	americana	deciduous	0.63	130
FRA_NI	Oleaceae	Fraxinus	nigra	deciduous	2.17	231
ABI_BA	Pinaceae	Abies	balsamea	deciduous	21.76	1185
LAR_LA	Pinaceae	Larix	laricina	deciduous	0.72	1185
PIC_GL	Pinaceae	Picea	glauca	deciduous	0.51	1185
PIC_MA	Pinaceae	Picea	mariana	deciduous	1.22	370
PIC_RU	Pinaceae	Picea	rubens	deciduous	2.06	1185
PIN_BA	Pinaceae	Pinus	banksiana	coniferous	0.03	1185
PIN_RE	Pinaceae	Pinus	resinosa	coniferous	0.01	1185
PIN_ST	Pinaceae	Pinus	strobus	coniferous	0.27	1185
TSU_CA	Pinaceae	Tsuga	canadensis	coniferous	1.89	1185
AME_CA	Pinaceae	Amelanchier	canadensis	coniferous	0.10	450
CRA_SP	Rosaceae	Crataegus	spp.	coniferous	0.01	450
MAL_SP	Rosaceae	Malus	spp.	coniferous	0.03	450
PRU_PE	Rosaceae	Prunus	pensylvanica	deciduous	0.58	450
PRU_SE	Rosaceae	Prunus	serotina	coniferous	1.49	25
SOR_DE	Rosaceae	Sorbus	decora	deciduous	0.03	450
POP_BA	Salicaceae	Populus	balsamifera	deciduous	1.22	613
POP_GR	Salicaceae	Populus	grandidentata	deciduous	2.62	613
POP_TR	Salicaceae	Populus	tremuloides	deciduous	6.01	613
SAL_SP	Salicaceae	Salix	discolor	deciduous	0.16	613
ACE_PE	Sapindaceae	Acer	pensylvanica	coniferous	0.37	227
ACE_RU	Sapindaceae	Acer	rubrum	deciduous	36.21	11371
ACE_SA	Sapindaceae	Acer	saccharum	deciduous	3.95	150
ACE_SP	Sapindaceae	Acer	spicatum	deciduous	0.01	227

ULM_AM	Ulmaceae	Ulmus	americana	deciduous	0.85	760

Table F.2: Eight functional traits of the 34 tree species of the Central Québec region: drought, shade, and water-logging tolerance, wood density, maximum tree height, seed mass, mode of reproduction (1 is vegetative reproduction, 2 is reproduction mostly by seed, and 3 is reproduction only by seed), and type of seed dispersal vector (i.e. gravity, endozoochorous, exozoochorous, bird, wind, water, or human-assisted). Vulnerability to be threaten is indicated by 1 and 0 otherwise and extracted from (Natural Resources Canada, 2017).

SppCode	Drought tolerance	Shade tolerance	Water-logging tolerance	Wood density	Max tree height	Seed mass	Mode reproduction	gravity	endozoochorous	exozoochorous	bird	wind	water	human	Pest threat
BET_AL	3.00	3.17	2.00	0.55	3000	0.001	2	0	0	0	0	1	0	0	0
BET_PA	2.02	1.54	1.25	0.48	3000	0.000	2	0	0	0	0	1	1	0	0
BET_PO	2.34	1.50	1.00	0.45	1000	0.000	2	0	0	0	0	1	0	0	0
OST_VI	3.25	4.58	1.07	0.63	1800	0.015	2	0	0	0	0	1	0	0	0
THU_OC	2.71	3.45	1.46	0.29	1500	0.001	1	0	1	0	0	1	0	0	0
FAG_GR	1.50	4.75	1.50	0.56	2500	0.283	1	1	1	1	1	0	0	0	0
JUG_CI	2.38	1.88	1.27	0.36	2500	15.129	2	1	1	0	0	0	0	0	1
TIL_AM	2.88	3.98	1.26	0.32	3500	0.095	2	1	1	0	1	1	0	0	0
FRA_AM	2.38	2.46	2.59	0.55	3000	0.045	2	0	0	0	0	1	1	0	1

FRA_NI	2.00	2.96	3.50	0.45	2000	0.047	2	0	0	0	0	1	1	0	1
ABI_BA	1.00	5.01	2.00	0.36	2500	0.008	2	0	1	0	0	1	0	0	1
LAR_LA	2.00	0.98	3.00	0.49	2438	0.002	2	0	1	0	0	1	0	0	0
PIC_GL	2.88	4.15	1.02	0.37	3000	0.002	2	0	1	0	0	1	0	0	1
PIC_MA	2.00	4.08	2.00	0.38	3000	0.001	1	0	0	0	0	1	0	0	1
PIC_RU	2.50	4.39	2.00	0.37	4000	0.003	2	0	1	0	0	1	0	0	1
PIN_BA	4.00	1.36	1.00	0.40	2700	0.003	3	0	1	0	1	1	0	0	0
PIN_RE	3.00	1.89	1.00	0.41	3700	0.008	3	0	1	0	1	1	0	0	0
PIN_ST	2.29	3.21	1.03	0.34	6700	0.017	3	0	1	0	1	1	0	0	0
TSU_CA	1.00	4.83	1.25	0.38	3000	0.002	3	0	1	0	0	1	0	0	0
AME_CA	2.52	2.86	1.39	0.66	800	0.005	NA	NA	NA	NA	NA	NA	NA	NA	0
CRA_SP	3.47	2.13	1.34	0.52	800	0.075	NA	0	1	0	1	0	0	0	0
MAL_SP	2.97	2.08	1.25	0.61	1150	0.023	2	0	1	0	0	0	0	1	0
PRU_PE	3.02	NA	NA	0.47	1200	0.032	2	0	1	0	1	0	0	0	0
PRU_SE	3.02	2.46	1.06	0.47	2400	0.094	2	1	1	0	1	0	0	0	0
SOR_DE	3.02	NA	NA	0.52	1829	0.017	2	0	0	0	1	0	0	0	0
POP_BA	1.77	1.27	2.63	0.31	3250	0.000	1	0	0	0	0	1	1	0	0
POP_GR	2.50	1.21	2.00	0.36	3500	0.000	1	0	0	0	0	1	1	0	0
POP_TR	1.77	1.21	1.77	0.35	3500	0.000	1	0	0	0	0	1	1	0	1
SAL_SP	1.63	1.61	3.88	0.36	1113	0.000	NA	0	0	0	0	1	1	0	0
ACE_PE	2.00	3.56	1.00	0.44	1000	0.037	2	0	0	0	0	1	0	0	0
ACE_RU	1.84	3.44	3.08	0.49	2500	0.023	2	0	0	0	0	1	1	0	0
ACE_SA	2.25	4.76	1.09	0.56	3500	0.069	2	0	0	0	0	1	1	0	0
ACE_SP	2.00	3.31	2.00	0.47	500	0.020	1	0	0	0	0	1	0	0	0
ULM_AM	2.92	3.14	2.46	0.46	3500	0.006	2	1	0	0	1	1	1	0	0

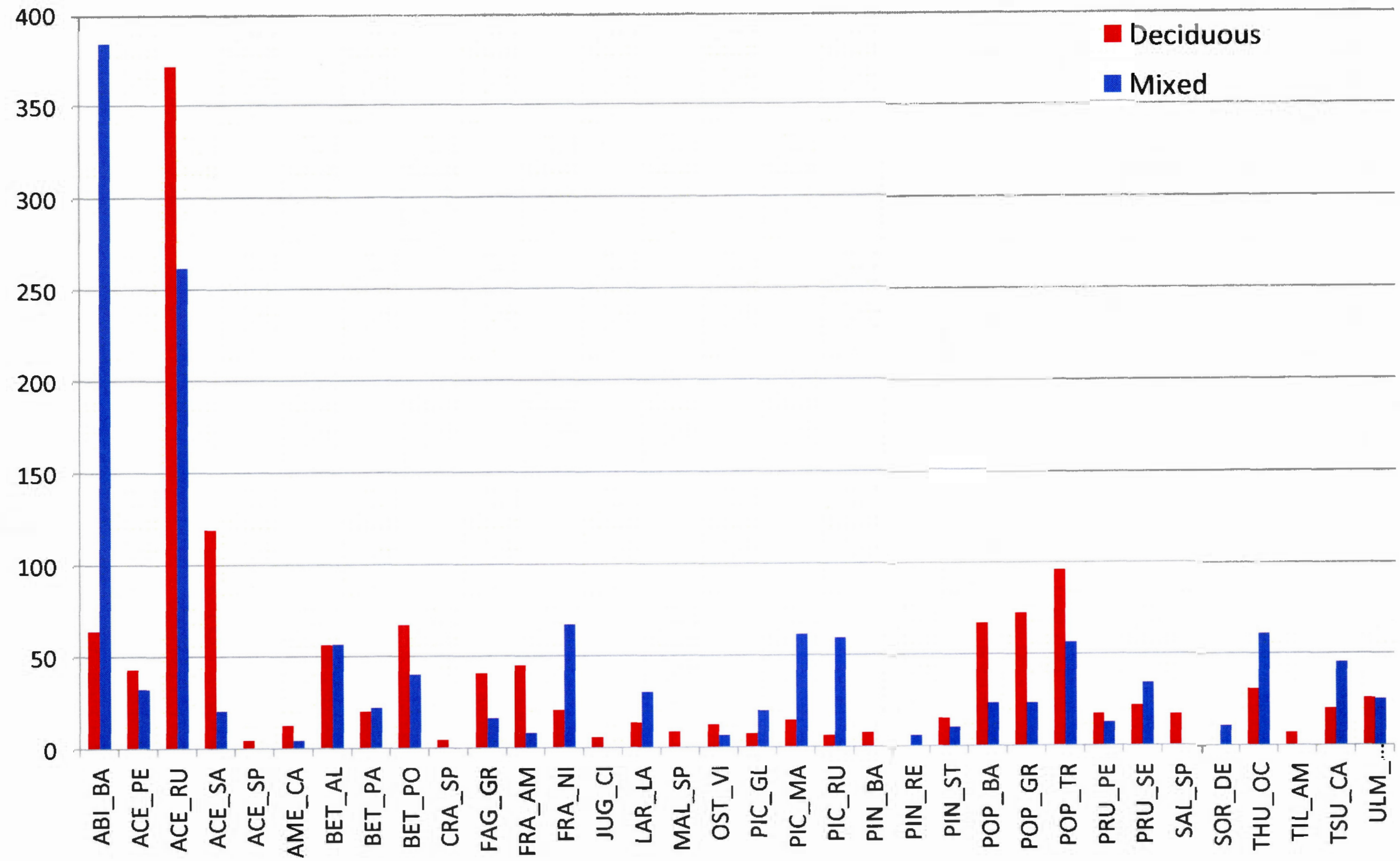

Figure F.1: Species relative abundance (number of trees per ha) per forest type derived from the species abundances sampled in the 42 sites of the Central Québec region.

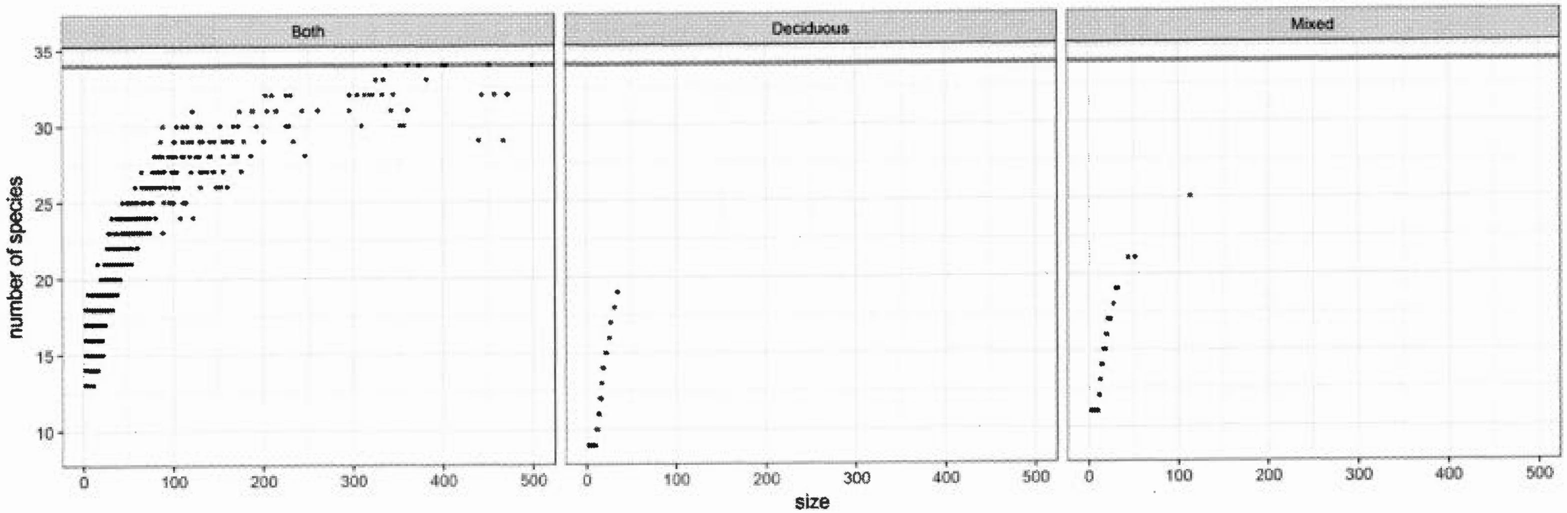

Figure F.2: Estimated species richness for the network patches according to the forest type and patch size. Grey line indicates the total species diversity (34) of the Central Québec region.

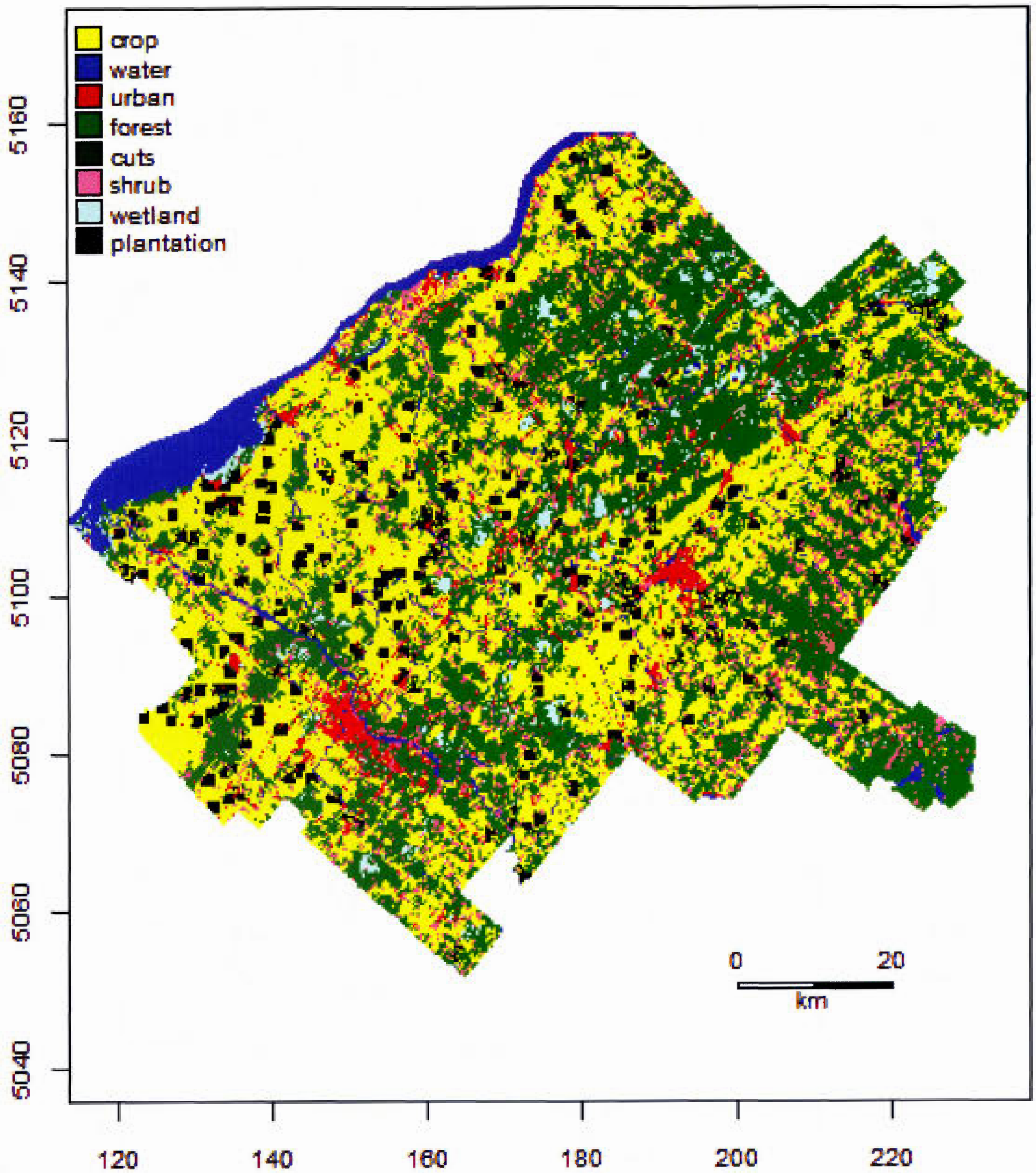

Figure F.3: 40 000 ha of forest allocated in the Central Québec region as random plantations of mean size 200 ha. Units on the *x*-axis and *y*-axis are in km.

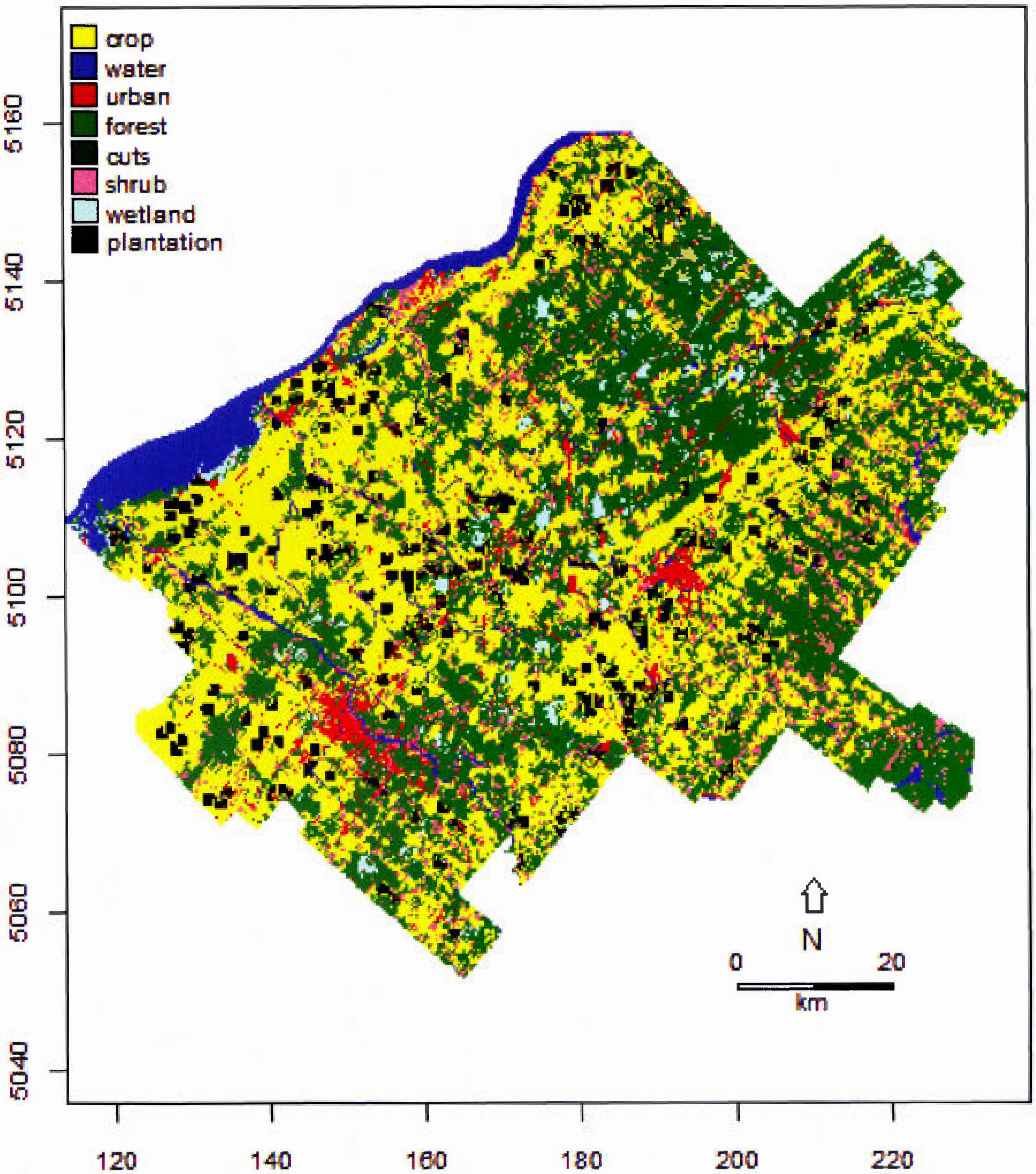

Figure F.4: 40 000 ha of forest allocated in the Central Québec region as riparian plantations of mean size 200 ha. Units on the x-axis and y-axis are in km.

[F.1] $RaoQ = \sum_i p_i \cdot [\sum_j p_j \cdot \delta_{ij}]$, where $0 < p_i \leq 1$ is the relative abundance of species *i* in a community, and $0 \leq \delta_{ij} \leq 1$ the functional dissimilarity between species *i* and *j*.

[F.2] $D = 1 - \sum_i p_i^2$, where $0 < p_i \leq 1$ is the relative abundance of species *i* in a community.

[F.3] $PC = \sum_{i=1}^{n} \sum_{j=1}^{n} f_i f_j p_{ij}^{*} / (\sum_i f_i)^2$, where *n* is the number of nodes in the network, f_i the *FDis* of node *i*, and p_{ij}^{*} the maximum probability of dispersion between nodes *i* and *j* (i.e. many path exist between *i* and *j*, p_{ij}^{*} is the most probable path).

[F.4] Let be *e* a symmetric matrix whose element e_{uv} is the fraction of all edges that link vertices in community *u* to vertices in community *v* of a graph. Then, $Q = \sum_u (e_{uu} - a_u^2)$ where $a_u = \sum_v e_{uv}$ is the fraction of edges that connect to vertices in community *u*.

[F.5] $BC_k^{PC} = \sum_i \sum_j f_i f_j p_{ij}^{*k}$ $(i, j \neq k, ij \in nm^{*})$ is the generalization of the BC metric for the node *k*, where f_i the *FDis* of node *i*, nm^{*} is the list of combinations of *i* and *j* ($i \neq j$) where *k* is included in the shortest path between *i* and *j*, and p_{ij}^{*k} is the maximum product probability between *i* and *j* belonging to nm^{*}.

ANNEX G

COMPLEMENTARY RESULTS - CHAPTER 3

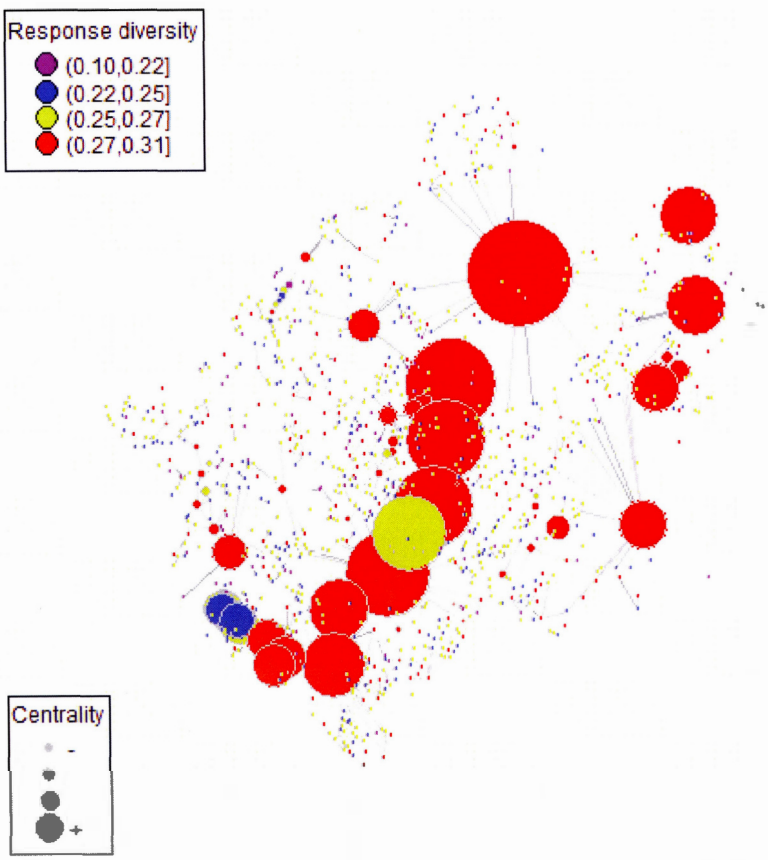

Figure G.1: Functional network of the Central Québec landscape after a drought episode. Node size is proportional to the betweenness centrality index BC^{PC} and node colour is as functional diversity index *FDis*.

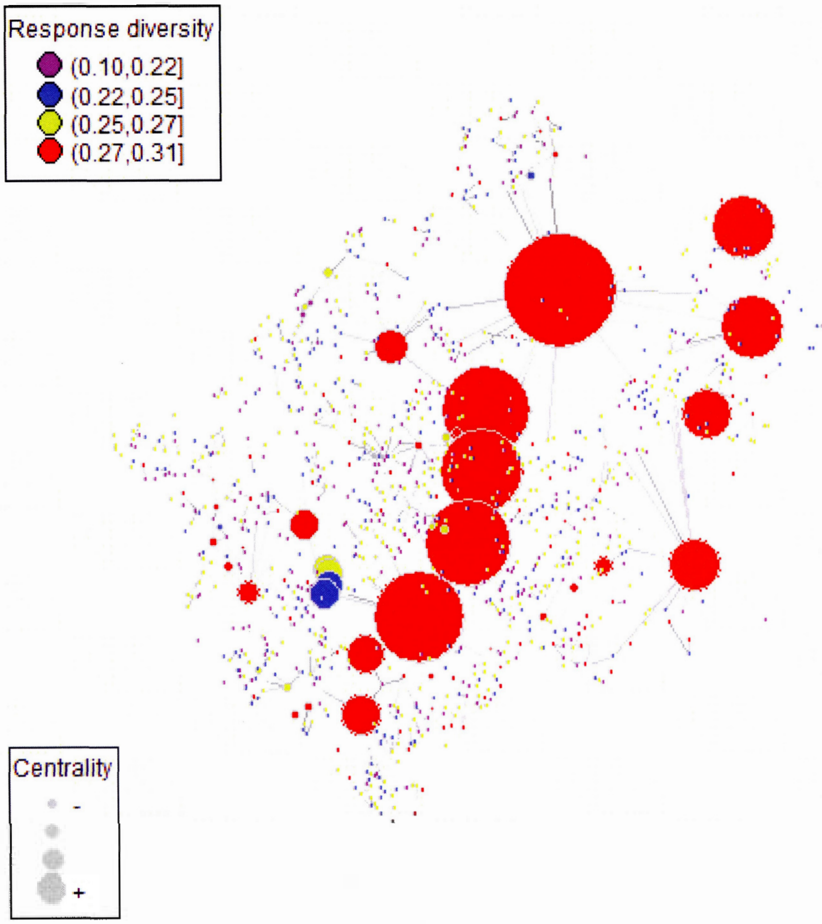

Figure G.2: Functional network of the Central Québec landscape after a pest outbreak. Node size is proportional to the betweenness centrality index BC^{PC} and node colour is as functional diversity index *FDis*.

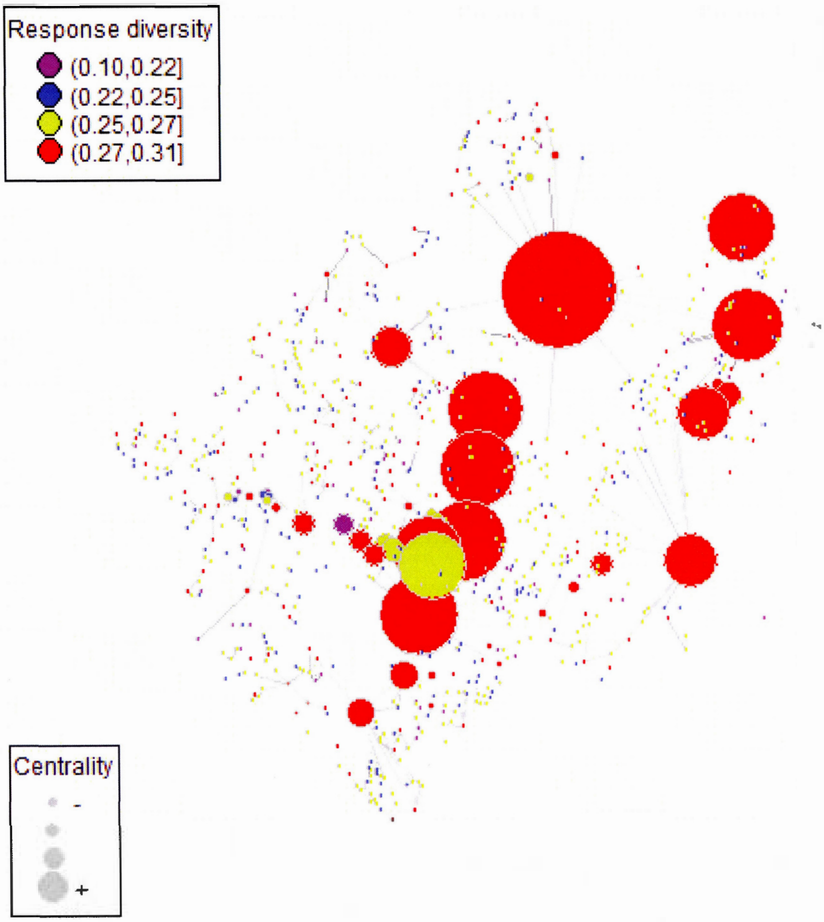

Figure G.3: Functional network of the Central Québec landscape after timber harvesting. Node size is proportional to the betweenness centrality index BC^{PC} and node colour is as functional diversity index *FDis*.

Table G.1: Values of the five resilience related properties: response diversity *RD*, functional redundancy *FR*, connectivity *PC*, modularity *Q*, and mean generalized betweenness centrality index BC^{PC} for the rural landscape of Central Québec region (*None* - *Reference*), the simulated landscapes under the functional enrichment strategy (*None* - *LowC10*, *HighC10*, *LessD10*, *LessD40*, and *LessD70*, see Table 3.1), and the simulated landscapes under the plantation strategy (*None* - *Rand10*, *Ripa10*, *Rand40*, *Ripa40*, *Rand70*, and *Ripa70*, see Table 3.1). Planted tree species in both strategies were selected according to three trait-based criteria: biodiversity enhancer (*B*), drought tolerant (*D*), or pest resistant (*P*). The same values are reported for the reference and simulated landscapes affected by drought (*Drought*), pest outbreak (*Pest*) and timber harvesting (*Harvest*) disturbances.

disturbance	**strategy**	**Criteria**	**RD**	**FR**	**PC**	**Q**	BC^{PC}
None	Reference		0.284	0.904	0.68	0.23	1.29
None	LowC10	B	0.291	0.900	0.78	0.23	1.69
None	LowC10	D	0.291	0.900	0.78	0.23	1.79
None	LowC10	P	0.290	0.902	0.78	0.25	1.46
None	HighC10	B	0.289	0.901	0.75	0.23	1.41
None	HighC10	D	0.289	0.901	0.76	0.22	1.43
None	HighC10	P	0.288	0.902	0.77	0.28	1.38
None	LessD10	B	0.294	0.899	0.83	0.25	1.73
None	LessD10	D	0.294	0.899	0.81	0.23	2.34
None	LessD10	P	0.292	0.900	0.84	0.23	1.82
None	LessD40	B	0.297	0.898	0.83	0.23	2.47
None	LessD40	D	0.296	0.898	0.85	0.23	2.11
None	LessD40	P	0.295	0.899	0.86	0.23	2.58
None	LessD70	B	0.297	0.897	0.86	0.23	2.38
None	LessD70	D	0.297	0.897	0.88	0.23	2.67
None	LessD70	P	0.295	0.899	0.88	0.28	2.45
None	Rand10	B	0.287	0.903	0.74	0.22	1.56
None	Rand10	D	0.286	0.903	0.77	0.23	1.57
None	Rand10	P	0.286	0.903	0.77	0.23	1.52
None	Ripa10	B	0.287	0.903	0.77	0.22	1.64
None	Ripa10	D	0.286	0.903	0.79	0.23	1.34
None	Ripa10	P	0.286	0.903	0.77	0.23	1.25

None	Rand40	B	0.293	0.900	0.78	0.23	1.88
None	Rand40	D	0.292	0.901	0.81	0.22	1.79
None	Rand40	P	0.291	0.901	0.82	0.23	2.14
None	Ripa40	B	0.294	0.899	0.83	0.22	1.51
None	Ripa40	D	0.291	0.901	0.83	0.22	1.76
None	Ripa40	P	0.291	0.901	0.83	0.22	1.62
None	Rand70	B	0.300	0.897	0.88	0.23	1.90
None	Rand70	D	0.296	0.899	0.90	0.23	2.26
None	Rand70	P	0.296	0.899	0.91	0.23	1.93
None	Ripa70	B	0.300	0.897	0.85	0.23	2.15
None	Ripa70	D	0.295	0.900	0.85	0.23	1.88
None	Ripa70	P	0.294	0.900	0.87	0.22	1.63
Drought	Reference		0.285	0.905	0.72	0.23	1.27
Drought	LowC10	B	0.293	0.901	0.80	0.25	1.84
Drought	LowC10	D	0.293	0.901	0.79	0.23	1.61
Drought	LowC10	P	0.291	0.902	0.81	0.23	1.53
Drought	HighC10	B	0.291	0.902	0.77	0.23	1.43
Drought	HighC10	D	0.291	0.902	0.78	0.23	1.70
Drought	HighC10	P	0.289	0.903	0.79	0.23	1.53
Drought	LessD10	B	0.296	0.899	0.84	0.23	1.51
Drought	LessD10	D	0.296	0.899	0.82	0.23	1.72
Drought	LessD10	P	0.294	0.901	0.87	0.25	1.96
Drought	LessD40	B	0.299	0.898	0.83	0.23	1.83
Drought	LessD40	D	0.298	0.898	0.85	0.23	2.01
Drought	LessD40	P	0.296	0.900	0.88	0.23	1.88
Drought	LessD70	B	0.299	0.897	0.87	0.23	2.40
Drought	LessD70	D	0.299	0.898	0.88	0.23	2.60
Drought	LessD70	P	0.296	0.900	0.88	0.23	2.03
Drought	Rand10	B	0.287	0.903	0.74	0.23	1.73
Drought	Rand10	D	0.287	0.904	0.76	0.23	1.86
Drought	Rand10	P	0.286	0.904	0.76	0.23	1.76
Drought	Ripa10	B	0.288	0.903	0.76	0.25	1.64
Drought	Ripa10	D	0.287	0.904	0.78	0.22	1.32
Drought	Ripa10	P	0.287	0.904	0.77	0.22	1.24
Drought	Rand40	B	0.295	0.900	0.80	0.23	1.74
Drought	Rand40	D	0.293	0.901	0.81	0.22	1.73
Drought	Rand40	P	0.292	0.902	0.83	0.22	2.17
Drought	Ripa40	B	0.295	0.900	0.83	0.22	1.61
Drought	Ripa40	D	0.292	0.902	0.83	0.22	1.74

Drought	Ripa40	P	0.292	0.902	0.83	0.22	1.74
Drought	Rand70	B	0.301	0.897	0.88	0.23	1.81
Drought	Rand70	D	0.297	0.900	0.89	0.23	2.16
Drought	Rand70	P	0.296	0.900	0.47	0.22	1.20
Drought	Ripa70	B	0.301	0.897	0.85	0.23	1.28
Drought	Ripa70	D	0.296	0.900	0.86	0.23	0.37
Drought	Ripa70	P	0.295	0.901	0.48	0.23	1.33
Pest	Reference		0.281	0.902	0.61	0.23	0.93
Pest	LowC10	B	0.289	0.899	0.73	0.23	1.55
Pest	LowC10	D	0.290	0.898	0.74	0.23	1.57
Pest	LowC10	P	0.289	0.899	0.75	0.23	1.61
Pest	HighC10	B	0.287	0.899	0.70	0.22	1.21
Pest	HighC10	D	0.287	0.899	0.70	0.23	1.43
Pest	HighC10	P	0.287	0.899	0.72	0.24	1.18
Pest	LessD10	B	0.293	0.897	0.81	0.23	1.44
Pest	LessD10	D	0.293	0.897	0.78	0.23	2.00
Pest	LessD10	P	0.293	0.898	0.81	0.23	1.96
Pest	LessD40	B	0.295	0.896	0.82	0.23	1.66
Pest	LessD40	D	0.295	0.896	0.83	0.23	1.78
Pest	LessD40	P	0.295	0.897	0.87	0.24	2.16
Pest	LessD70	B	0.296	0.896	0.84	0.23	2.10
Pest	LessD70	D	0.296	0.896	0.87	0.23	2.09
Pest	LessD70	P	0.296	0.897	0.87	0.27	2.13
Pest	Rand10	B	0.284	0.900	0.71	0.22	1.57
Pest	Rand10	D	0.284	0.901	0.72	0.22	1.64
Pest	Rand10	P	0.284	0.901	0.73	0.23	1.60
Pest	Ripa10	B	0.285	0.900	0.73	0.22	1.58
Pest	Ripa10	D	0.284	0.901	0.74	0.23	0.87
Pest	Ripa10	P	0.284	0.901	0.73	0.22	1.42
Pest	Rand40	B	0.293	0.898	0.78	0.22	1.85
Pest	Rand40	D	0.291	0.898	0.78	0.22	1.80
Pest	Rand40	P	0.290	0.899	0.79	0.23	2.17
Pest	Ripa40	B	0.293	0.897	0.79	0.22	1.69
Pest	Ripa40	D	0.290	0.899	0.82	0.22	2.31
Pest	Ripa40	P	0.291	0.899	0.79	0.22	1.67
Pest	Rand70	B	0.299	0.895	0.86	0.23	1.87
Pest	Rand70	D	0.296	0.897	0.86	0.23	1.48
Pest	Rand70	P	0.296	0.897	0.88	0.23	2.18
Pest	Ripa70	B	0.299	0.895	0.86	0.23	1.24

Pest	Ripa70	D	0.295	0.897	0.85	0.23	1.98
Pest	Ripa70	P	0.294	0.898	0.87	0.22	-4.78
Harvest	Reference		0.284	0.904	0.52	0.25	1.29
Harvest	LowC10	B	0.290	0.901	0.61	0.24	1.64
Harvest	LowC10	D	0.290	0.901	0.59	0.25	1.70
Harvest	LowC10	P	0.289	0.902	0.67	0.25	1.74
Harvest	HighC10	B	0.289	0.902	0.59	0.30	1.49
Harvest	HighC10	D	0.289	0.902	0.61	0.24	1.57
Harvest	HighC10	P	0.288	0.902	0.66	0.24	1.48
Harvest	LessD10	B	0.293	0.899	0.66	0.23	1.87
Harvest	LessD10	D	0.293	0.899	0.59	0.24	1.88
Harvest	LessD10	P	0.292	0.901	0.70	0.23	1.83
Harvest	LessD40	B	0.295	0.899	0.70	0.26	2.49
Harvest	LessD40	D	0.295	0.899	0.70	0.25	2.12
Harvest	LessD40	P	0.294	0.900	0.78	0.24	2.12
Harvest	LessD70	B	0.296	0.898	0.75	0.23	2.35
Harvest	LessD70	D	0.296	0.898	0.70	0.24	2.05
Harvest	LessD70	P	0.294	0.900	0.75	0.37	2.24
Harvest	Rand10	B	0.287	0.903	0.54	0.25	1.41
Harvest	Rand10	D	0.286	0.903	0.58	0.24	1.29
Harvest	Rand10	P	0.286	0.903	0.59	0.23	1.44
Harvest	Ripa10	B	0.287	0.902	0.64	0.22	1.73
Harvest	Ripa10	D	0.286	0.903	0.65	0.24	1.57
Harvest	Ripa10	P	0.286	0.903	0.61	0.22	1.42
Harvest	Rand40	B	0.294	0.900	0.40	0.22	1.40
Harvest	Rand40	D	0.292	0.901	0.40	0.22	1.47
Harvest	Rand40	P	0.291	0.901	0.40	0.22	1.45
Harvest	Ripa40	B	0.294	0.899	0.48	0.23	1.51
Harvest	Ripa40	D	0.291	0.901	0.49	0.22	1.75
Harvest	Ripa40	P	0.291	0.901	0.49	0.22	1.53
Harvest	Rand70	B	0.300	0.897	0.71	0.33	1.88
Harvest	Rand70	D	0.296	0.899	0.69	0.25	1.76
Harvest	Rand70	P	0.296	0.899	0.78	0.24	2.06
Harvest	Ripa70	B	0.300	0.896	0.63	0.25	1.64
Harvest	Ripa70	D	0.295	0.900	0.63	0.25	1.48
Harvest	Ripa70	P	0.295	0.900	0.66	0.25	1.63

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