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**FOREST DYNAMICS:
SPACE-TIME PATTERNS OF BIODIVERSITY
UNDER CHANGING MANAGEMENT**

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*Abeti, betulle, paesi, città, betulle, paesi, corsi d'acqua gelati,
ragazzi sui pattini, una slitta nella pianura, una casupola, abeti.
Allegria portava la vista di una grossa lepre che sbucava spaurita
dalle siepi paraneve che fiancheggiavano la ferrovia;
stupore e poesia i piccoli branchi di caprioli che dall'orlo dei boschi
guardavano passare il nostro treno coperto di ghiaccioli
e pareva impossibile che nel mondo ci fosse la guerra e noi armati.*

MARIO RIGONI STERN

Preface

This thesis is the product of a three year PhD project at the BiGeA Department of the University of Bologna, based at the research group of Plant Diversity, Ecology and Conservation. The thesis has been supervised by Prof. Alessandro Chiarucci, with Dr. Juri Nascimbene collaborating as co-supervisor though not officially affiliated with the project.

While the base has been the research group in Bologna, during the PhD I spent a period of three months at the Center for Macroecology Evolution and Climate (CMEC), University of Copenhagen, developing part of the project under the supervision of Prof. Jacob Heilmann-Clausen.

Further I had the opportunity to attend various courses among other institutions, learning and being inspired by different approaches to the research: the University of Lisbon – Portugal (course “*Measuring Biodiversity: How to get data, assess its quality and measure different aspects of diversity*”), the University of South Bohemia – Czech Republic (course “*Species traits: a functional approach to biodiversity, from organisms to ecosystems - 6th edition*”), the Science School at La Palma (Canary Islands, Spain) organized by the University of Bayreuth – Germany, the Edmund Mach Foundation (San Michele all’Adige, Trento, Italy).

The thesis consists of two parts. The first part consists of three chapters dealing with methods to assess spatial and temporal patterns of plant diversity within forest ecosystems and protected areas. The second part consists of two chapters related to the effects of management on forest biodiversity. Two chapters have already been published by international journals. The remaining three chapters are written as scientific research papers and close to the submission process.

The development of this PhD project has been a unique opportunity for improving my skills in planning survey designs, conducting field samplings, coordinating team works and using tools and software for data management and analysis (especially R and QGIS).

I presented the results of my project at the following conferences: 25th EVS Meeting 2016, Rome – Italy (poster), 51st SISV Congress 2017, Bologna – Italy (poster), 2nd International Conference on Forests 2017, Bavarian Forest National Park – Germany (poster), SBI Conference 2018, Fisciano – Italy (poster), SLI Conference 2018, Pistoia – Italy (oral presentation), IUFRO Conference 2018, Viterbo – Italy (oral presentation).

While being a PhD student I have also acted as co-supervisor on one master thesis (Chiara Suanno), four bachelor projects (Elena Dalla Dea, Erica Salvatelli, Martina Marei Viti, Edoardo Ziviani), as well as assisted with field activity for the courses of *i*) Vegetation Ecology (graduate level, years 2016 and 2017) and *ii*) Phytogeography (undergraduate level, year 2018).

Chiara Lelli
Bologna, Italy, October 2018

Contents

	<i>page</i>
Preface	3
Abstract	5
Overview	6
Chapter I	17
<i>Are available vegetation data suitable for assessing plant diversity? A study case in the Foreste Casentinesi National Park (Italy)</i>	
Chapter II	30
<i>Comparing preferential and probabilistic surveys to assess and monitor plant diversity in Protected Areas</i>	
Chapter III	45
<i>How mountain forests are changing: Resurvey of historical vegetation data in the Northern Apennines (Italy)</i>	
Chapter IV	60
<i>Response of vascular plants and epiphytes to management and abandonment in mountain beech forests of the Northern Apennines (Italy)</i>	
Chapter V	79
<i>Biodiversity response to forest structure and management: Comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation</i>	
Acknowledgements	104

Abstract

Aims: With this thesis we aimed to enhance the conservation of forest biodiversity, investigating: (i) The suitability of sampling methods for assessing patterns and trends of plant diversity; (ii) The effects of forest management and abandonment on biodiversity, focusing on European beech and other mountain forest habitats and by using a multi-taxon approach.

Main study area: Foreste Casentinesi National Park (Northern Apennines, Italy).

Methods: (i) In *Chapter I* we generated a georeferenced data set by assembling all the available forest vegetation data (386 phytosociological records from 1934 to 2007) collected in the study area, to investigate their spatial and temporal patterns. In *Chapter II* we carried out a probabilistic survey to analyze the consistency between preferential and probabilistic samplings for spatial and ecological properties. In *Chapter III*, we performed a resurvey study based on the oldest vegetation data included in the georeferenced data set, 22 vegetation plot data recorded between 1934 and 1961 in three mountain forest types (i.e., beech, chestnut and oak forests) to assess changes in species richness, composition and forest structure. (ii) In *Chapter IV* we analyzed the effects of management vs. abandonment focusing on mountain beech forests (*Fagus sylvatica* L.) and targeting three species groups (i.e., vascular plants, epiphytic lichens and bryophytes). In *Chapter V*, we investigated the consistency between richness and trait-based diversity metrics in capturing the effects of management-related habitat factors on biodiversity. We analyzed a management-related environmental gradient, from long unmanaged to even-aged managed stands of European beech forests in Denmark, targeting five species groups (vascular plants, epiphytic lichens and bryophytes, saproxylic fungi and birds).

Results: (I) The preferential survey provides a biased estimation of patterns and trends of plant diversity. (II) In contrast, a probabilistic method is more suitable for a statistically representative picture of plant communities, but it does not allow recording some biodiversity features that are spatially localized and important for assessing the conservation status of species and habitats, as it is done by the preferential approach. Therefore, both sources of information should be considered to maximize the effectiveness of plant diversity assessment and monitoring. (III) Dynamics assessed in the resurvey study reflects a widespread process of abandonment of mountains in the second half of 20th century. Forests are getting taller and darker, with a reduction in the species richness of the herb layer, the replacement of light-demanding species with more shade-tolerant ones, and a more mixed composition of the chestnut and oak forests, including several tree species typical of mixed-broadleaved forests. (IV) Different species groups show contrasting responses to management and abandonment, indicating also different rates of recovery over time where the legacy of past management is still strongly detectable in forest structure. (V) At present, the occurrence of conservation-relevant species is a sound and relevant metric for planning and evaluating conservation actions, especially for less studied organism groups (e.g., saproxylic fungi and epiphytes).

Conclusions: The use of proper sampling methods and metrics for biodiversity assessment is baseline for an effective conservation planning and much effort should be addressed to define standardized and widely accepted methods. A multi-taxon approach is highly recommended to avoid misleading conclusion for conservation and further studies to identify suitable indicators of overall biodiversity through a functional approach may support rapid assessment methods, which are needed for practical conservation.

Overview

<i>Contents</i>	<i>page</i>
Introduction	6
Structure of this thesis	9
Study area	9
Methods	11
Conclusions	11
References	14

Introduction

Forests are defined as: “Lands spanning more than 0.5 hectares with trees higher than 5 meters and a canopy cover of more than 10 percent, or trees able to reach these thresholds *in situ*. They do not include land that is predominantly under agricultural or urban land use” (FAO, 2018).

Accordingly, trees are assumed as the major determinants of forest areas, irrespective of their origin, whether natural or planted, and of other components of the ecosystem.

This is a static definition to describe a system that is, instead, characterized by dynamicity and processes. Indeed, an increasing attention is paid on preserving and enhancing the functionality of forests (Kraus and Krumm, 2013) as macro-organisms characterized by a complex network of biotic and abiotic interactions. Functions are any exchanges of energy that support the integrity and maintenance of ecosystems, resulting from the interactions between structures and processes (Díaz et al., 2006; Brockerhoff et al., 2017). They represent the basis for the provision of several biospheric and social services for the human well-being (Brockerhoff et al., 2017; FAO and EFI, 2015; Mori et al., 2017). There is increasing consensus that biodiversity is fundamental for ecosystem functioning, as well as for the provision of ecosystem services (Hooper et al., 2012; Harrison et al., 2014). Boosted by these reasons and by the increasing awareness of its decline, protection of forest biodiversity has received increasing attention in the last decades and it is currently related to the sustainable use of forests (Kraus and Krumm, 2013).

Biodiversity assessments are largely based on the measure of species diversity (i.e., richness and composition) for which a critical node consists in the use of proper sampling methods for an unbiased quantification of diversity, in order to provide good quality data for a scientifically sound conservation planning (Chiarucci et al., 2011; Carli et al., 2018).

Focusing on vascular plants, there is still a lack of data systematically collected according to quantitative and comparable methods and this is weakening the effectiveness of assessments and monitoring activities (e.g., Lengyel et al., 2008; Bacaro et al., 2009). A potentially important source of information is represented by past vegetation data collected at plot scale according to the phytosociological approach (Braun-Blanquet, 1964; Jansen et al., 2012; Chytrý et al., 2014).

Notwithstanding, the suitability of this type of data for assessing spatial patterns of species diversity, and for setting up a habitat monitoring system, is under debate, with studies stressing pros and cons of this approach (e.g., Diekmann et al., 2007; Lepš, 2007; Roleček et al., 2007).

In the first part of this thesis, we aimed to contribute to a better understanding of the limits and potentiality of this type of data, by themselves alone (*Chapter I*), or by a direct comparison with a statistically more sound probabilistic sampling method (*Chapter II*). For this goal, we generated a georeferenced data set by assembling all the available forest vegetation data from published or unpublished sources (386 phytosociological records from 1934 to 2007), collected within an Italian National Park (Foreste Casentinesi NP), to analyze their spatial and temporal distribution. To overcome some pitfalls related to the phytosociological approach (Chytrý, 2001), probabilistic methods are considered as a possible alternative (e.g., Roleček et al., 2007), but few studies compared data collected using both approaches in the same area, thus hindering the evaluation of their relative suitability. Therefore, we specifically designed a probabilistic survey for the same study area, according to a tessellation stratified random sampling method, to directly compare spatial and ecological information obtained by the preferential and the probabilistic surveys.

Historical vegetation data are increasingly used in resurvey study, representing a valuable source of information for detecting habitat changes over time that may inform conservation actions (Kapfer et al., 2017). In *Chapter III*, we performed a resurvey study for investigating vegetation changes in the mountain forests of the Northern Apennines (Italy). In fact, we retrieved and digitized historical vegetation data collected between the 1934 and 1961 (Zangheri, 1966) that are much older than the majority of the vegetation data available for resurvey studies (Jansen et al., 2012), thus providing the unique opportunity of investigating changes over a long time, in the light of a widespread abandonment of mountain settlements due to socio-economic changes in the second half of the 20th century (Vacchiano et al., 2017; Jepsen et al., 2015). Indeed, in Europe forest management is a dominant driver of ecological dynamics, in most cases outweighing by far the effects of macro-ecological constraints (Brown et al., 2013) and shaping structure and composition of forest ecosystems for millennia (Bengtsson et al., 2000; Brunet et al., 2010; Kulakowski et al. 2017). This long history of landscape and forest use has altered almost all the European forests, with few and fragmented remnant pristine forests covering only the 0.7% of the whole forested area (Sabatini et al., 2018). These remnants are refugia for several sensitive and narrow-range species that are virtually lacking in managed stands (Brunet et al., 2010). The value of these untouched forests for biodiversity and functioning conservation is recognized, and set-asides represent a key element in integrative conservation strategies (Kraus and Krumm, 2013). In the last decades a process of land-use polarization is being observed in Europe, with some forests, especially plantations, that are being managed more intensively than in the past due to an increasing demand of wood product,

while other forests mostly located in less-accessible places, montane or protected areas, are currently managed less intensively than in the past, or even abandoned (Jepsen et al., 2015; Burrascano et al., 2016). The value of abandonment for biodiversity is debated: from one hand, it is considered as part of a rewilding strategy aimed to promote the recovery of natural processes, structure and composition (Sitzia et al., 2015; Watson et al., 2018). On the other hand, it is considered the driver of the loss of cultural forests hosting peculiar species (Bollmann and Braunisch, 2013). Several studies investigated the response of forest species to forest management as compared to abandonment, showing contrasting results depending on the investigated species groups as well as on the forest type, management conditions and spatial/temporal scale of investigation (e.g., Paillet et al., 2010; Schall et al., 2018). These studies highlight the need of further research on this issue, for improving forest sustainability and biodiversity conservation. In particular, much effort should be devoted to the use of a multi-taxon approach that is increasingly recommended for guiding conservation actions, since mechanisms which shape species assemblages are not identical among species groups (Flensted et al., 2016). Therefore, in *Chapter IV* we compared the effects of forest management and abandonment focusing on the mountain beech forests (*Fagus sylvatica* L.) of the Northern Apennines (Italy) and targeting three species groups with different habitat requirements. Besides vascular plants, we investigated also the response of usually neglected organisms, as in the case of epiphytic lichens and bryophytes, to forest structure, topographic, and climatic gradients.

Finally, besides sampling methods, another critical node for assessing status and trends of forest biodiversity is the use of proper metrics for its quantification. The choice of biodiversity metrics can substantially affect the evaluation of the effectiveness of conservation activities. However, their relative sensitivity is still scarcely investigated, especially in a multi-taxon framework, hindering practical application. To contribute filling this gap, in *Chapter V* we investigated the consistency between richness (i.e., total species richness, richness of conservation-relevant species) and trait-based diversity (i.e., functional diversity) metrics in capturing the effects of management-related habitat factors on biodiversity. For this purpose we analyzed a management-related environmental gradient, from long unmanaged to even-aged managed stands of European beech forests in Denmark, targeting five species groups (vascular plants, epiphytic lichens and bryophytes, saproxylic fungi and birds).

Overall, with this thesis we aimed to contribute to enhance the conservation of forest biodiversity, investigating: (i) the suitability of sampling methods for assessing patterns and trends of plant diversity; (ii) the effects of management and abandonment on biodiversity, focusing on European beech forests with a multi-taxon approach.

Structure of this thesis

This thesis consists of five chapters written as scientific papers. Each chapter is independent, but linked to the others following the common thread described in the general introduction. *Figure 1* synthesizes the structure of the thesis, underlining the main questions and targets of the chapters.

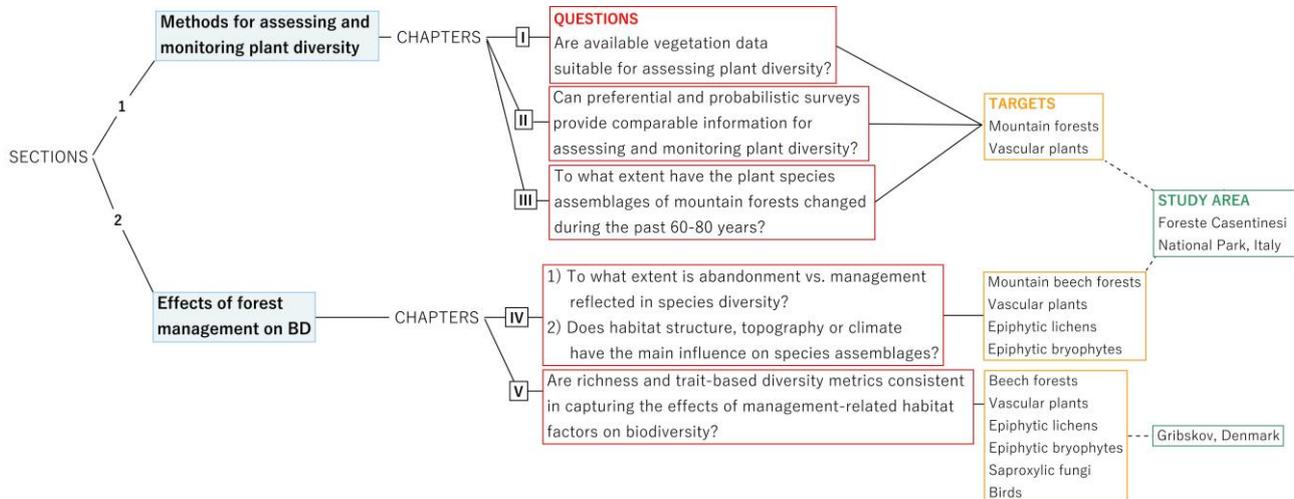


Figure 1 Structure of the thesis. BD: Biodiversity. For each chapter, the main questions, targets and study area are shown.

Study areas

Most of this thesis has been developed using data collected within a major protected area in Italy, the Foreste Casentinesi National Park (*Figure 2*). This protected area ($43^{\circ}51'35.3''N$; $11^{\circ}45'32.2''E$) extends over an area of about 368.43 km^2 , stretching across the ridge of the northern Apennines from 400 m a.s.l. to 1657 m a.s.l.

It represents a core site for studying and preserving forest biodiversity. In fact, it is mostly covered by forests of different types, ages and naturalness, ranging from the Integral Reserve of Sasso Fratino Unesco Heritage (Bottacci, 2009) to intensively managed stands (i.e., coppices and high forests), in a system characterized by high forest continuity and connectivity. At higher elevation (up to 900-1000 m a.s.l.) European beech forests (*Fagus sylvatica* L.) dominate in pure and mixed formations with *Acer pseudoplatanus* L. and *Abies alba* Mill., covering the 40% ca of the protected area, while at lower and intermediate elevation mixed broadleaf formations prevail, including oaks (*Quercus cerris* L., and *Q. pubescens* Willd.), chestnuts (*Castanea sativa* Mill.), hop hornbeams (*Ostrya carpinifolia* Scop.), and the Italian maple (*Acer opalus* Mill.), covering the 36%. Conifer plantations cover 15% of the protected area, mostly composed of silver fir (*Abies alba* Mill.) and black pines (*Pinus nigra* J.F. Arnold.). Spontaneous silver fir stands can be found also in beech-dominated areas, covering 6% of the park. Pure chestnut (*Castanea sativa*) formations and riparian forests dominated by common alder (*Alnus glutinosa* (L.) Gaertn.) are rare, covering 1.7% of the park surface (Viciani and Agostini, 2008). The study presented in Chapter V, developed at the

University of Copenhagen, has been based on data collected in Gribskov, one of the largest coherent forests in Denmark, covering an area of almost 6.000 ha. These forests are shaped by two centuries of timber oriented forestry, with European beech and Norway spruce (*Picea abies* (L.) H. Karst.) dominating and largely found as even-aged monocultures. Only small remnants of old-growth forests are left, mainly as stands smaller than 5 ha.

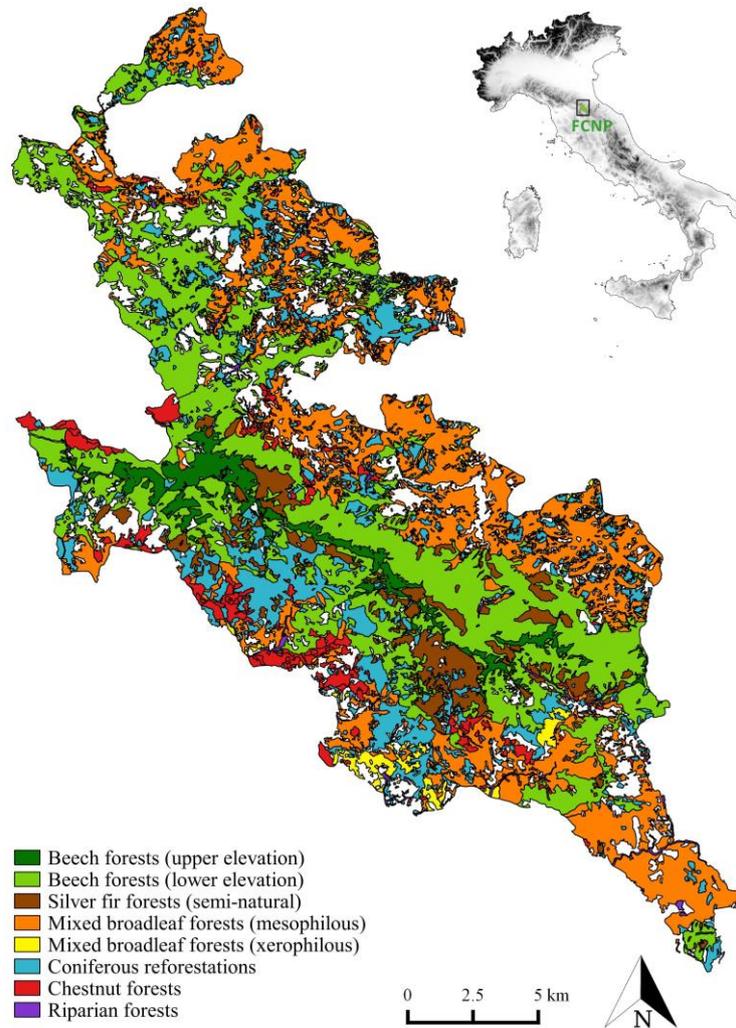


Figure 2 Main study area of this thesis: The Foreste Casentinesi National Park, Italy (FCNP). The gradient from black to white indicates upper to lower elevations, respectively. The protected area is located along the Apennines ridge. Forest types are shown with different colours (source: Viciani and Agostini, 2008, simplified).

Methods

Sampling and analytical methods and data used in each chapter are synthesized in *Figure 3*. All analyses were performed with the R statistical software version 3.4.2 (R Core Team, 2017).

Results are reported and discussed in detail in each chapter.

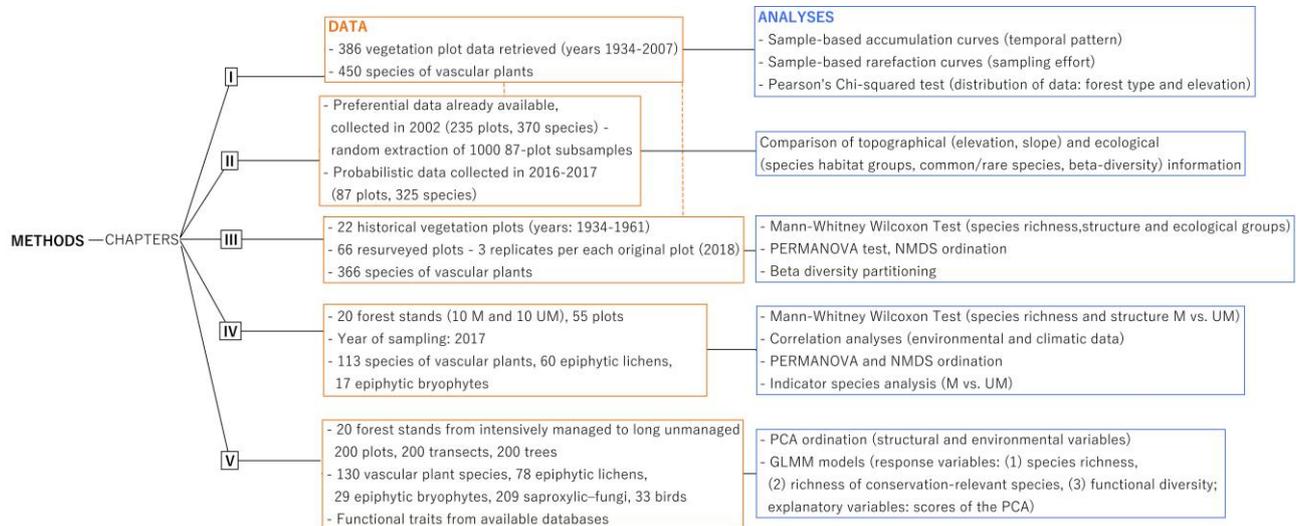


Figure 3 Summary of data, sampling methods and analytical methods adopted for each chapter. FCNP: Foreste Casentinesi National Park; M: Managed stands; UM: Abandoned stands.

Conclusions

The assessment and monitoring of forest biodiversity using proper sampling methods and metrics is baseline for an effective conservation planning.

Focusing on the sampling methods for plant diversity, our findings (*Chapter I* and *II*) corroborate the view that the widely used phytosociological approach provides a biased estimation of patterns and trends of plant diversity, due to intrinsic methodological pitfalls especially linked to the preferential location of sampling units (Chytrý, 2001; Lájér, 2007). In contrast, a probabilistic method (*Chapter II*) is more suitable for a statistically representative picture of plant communities, providing information spatially balanced. However, some biodiversity features (e.g., rare species or habitat specialist species) that are spatially localized and important for assessing the conservation status of species and habitats, are more difficultly recorded with the probabilistic method rather than with the preferential one (Palmer et al., 2002). Therefore, further effort needs to be addressed (i) to improve probabilistic methods in order to increase their ecological representativeness (Roleček et al., 2007), and/or (ii) to define a standardized and accepted way to integrate expert knowledge into probabilistic sampling methods, or to include simple and easy to measure auxiliary variable in adaptive sampling, as suggested and tested in recent studies (e.g., Chiarucci et al., 2018; Gattone et al., 2018).

Even if phytosociological data are not completely suited for a standardized assessment of plant diversity and for monitoring purposes, historical vegetation data collected according to this traditional approach are an invaluable source of information for resurvey studies aimed to investigate vegetation and environmental changes over the past decades (Kapfer et al., 2017). Our resurvey study (*Chapter III*) based on historical vegetation plot data located in three mountain forest types (i.e., beech, chestnut, and oak forests) of the Northern Apennines (Italy), revealed a general trend of structural and compositional changes (i.e., increase height and coverage of trees, decrease in species richness of herb and shrub layers, increase of shade-tolerant species and decrease of light-demanding ones, chestnut and oak forest converging into mixed-broadleaved forests in terms of species composition) linked to the abandonment of mountain settlements in the second half of the 20th century (Vacchiano et al., 2017). The positive effect of abandonment for enhancing and preserving forest biodiversity is context-dependent. Indeed, abandonment implies the loss of cultural forests shaped by centuries of human use, as part of a traditional agro-silvicultural land-use system, such as coppices or chestnut orchards (Pezzi et al., 2011; Mölder, 2015; Müllerová et al., 2015). Cultural forests have become the optimal habitat for species and assemblages threatened by the withdrawal of these traditional management systems (Bollmann and Braunisch, 2013).

On the other side, several studies consider forest abandonment as a first positive step for a gradual recovery of old-growth attributes (Paillet et al., 2010; Sitzia et al., 2015; Kulakowski et al., 2017; Watson et al., 2018). Old-growth forests, which are currently too rare and fragmented across Europe (Sabatini et al., 2018), have an outstanding importance for preservation of natural processes, structures and community composition, acting as refugia for demanding and narrow-range species threatened by management disturbances (Brunet et al., 2010). However, unmanaged forests where the legacy of past management is still strongly detectable in the forest structure are mostly not different by managed forests, like in our study focused on mountain beech forests of the Northern Apennines (*Chapter IV*). This applies as well to most unmanaged forests in Europe which had been managed over centuries prior to set-aside (Schall et al., 2018). In fact, overall ecosystem recovery is a long-term process and different species groups exhibit different rates of recovery over time (Nascimbene et al., 2013; Spake et al., 2015; Kaufmann et al., 2017). This underlines the importance of (i) considering the relative temporal scale of investigation for avoiding misleading conclusions for conservation; (ii) adopting a multi-taxon approach (*Chapter IV and V*) since species groups with different requirements respond differently to changes, showing also contrasting patterns (Paillet et al., 2010; Schall et al., 2018). For instance, a decrease in species richness of vascular plants, as measured in our resurvey study (*Chapter III*), is not necessarily consistent with a decrease in overall biodiversity and in the conservation status of the forests (Paillet et al., 2010). In contrast, higher plant species richness may be considered an indicator of disturbance rather than of

conservation status (Boch et al., 2013), since plants may benefit from resource increase also following moderate disturbance by management (Roberts, 2004; Christensen and Heilmann-Clausen, 2009). This also supports the view that the use of different metrics of biodiversity may strongly influence the evaluation of conservation activities. Comparing the consistency of three main metrics (i.e., species richness, richness of conservation-relevant species and functional diversity) to inform about the effects of management-related habitat factors on biodiversity in European beech forests (*Chapter V*), we found that at present the occurrence of conservation-relevant species is the most sound and relevant metric for planning and evaluating conservation actions, especially for less studied organism groups (e.g., saproxylic fungi and epiphytes). The functional approach is promising for rapid biodiversity assessments, which are needed for practical conservation. In fact, the multi-taxon approach, which is increasingly recommended for guiding conservation actions, still has practical limits: identifying species across many relevant taxonomic groups is time and resource consuming, and often impractical in broad-scale monitoring and research. In this context, the identification and validation of suitable indicators of overall biodiversity is fundamental for conservation. The use of a functional approach has considerable potential in this context, if suitable recognisable and responsive traits can be identified (e.g., Aragón et al., 2016). However, for reaching this goal a preliminary selection and subsequent testing of responsive traits is required for each species group, which are only partially available and mainly for more well studied groups. Therefore, further studies are needed for identifying the best suited traits which may help in effective and rapid biodiversity assessments.

Overall, an effective conservation of biodiversity should be planned considering the complexity of forest systems, with mechanisms and interactions acting at multiple spatial scales, and long-term processes (e.g., Kaufmann et al., 2017; Schall et al., 2018). In a landscape matrix that is strongly human modified, human pressures and economical demands often require a compromise between conservation and commodity production (Kraus and Krumm, 2013) and integrative approaches are considered an opportunity to avoid homogenization and fragmentation of forest systems at multiple spatial scales (Vandekerkhove et al., 2013). In this framework, the conservation of forest biodiversity should be planned at landscape level (Schall et al., 2018), considering the contribution of traditional forest practices, as well as of other sustainable uses of the forests, to structural and compositional diversity (Bollmann and Braunisch, 2013), together with the protection of set-aside areas for allowing the recovery of natural dynamics over long time.

References

- Aragón, G., Belinchón, R., Martínez, I., Prieto, M., 2016. A survey method for assessing the richness of epiphytic lichens using growth forms. *Ecological Indicators* 62, 101–105. <https://doi.org/10.1016/j.ecolind.2015.11.034>
- Bacaro, G., Baragatti, E., Chiarucci, A., 2009. Using taxonomic data to assess and monitor biodiversity: are the tribes still fighting? *Journal of Environmental Monitoring* 11, 798. <https://doi.org/10.1039/b818171n>
- Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *Forest Ecology and Management* 132, 39–50. [https://doi.org/10.1016/S0378-1127\(00\)00378-9](https://doi.org/10.1016/S0378-1127(00)00378-9)
- Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A., Hessenmöller, D., Kalko, E.K.V., Linsenmair, K.E., Pfeiffer, S., Pommer, U., Schöning, I., Schulze, E.D., Seilwinder, C., Weisser, W.W., Wells, K., Fischer, M., 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. *Basic and Applied Ecology* 14, 496–505. <https://doi.org/10.1016/j.baae.2013.06.001>
- Bollmann K., and Braunisch V., 2013. To integrate or to segregate: balancing commodity production and biodiversity conservation in European forests. In: Kraus, D., Krumm, F., 2013. *Integrative approaches as an opportunity for the conservation of forest biodiversity*, European Forest Institute.
- Bottacci A. (Ed.) (2009). *La Riserva Naturale Integrale di Sasso Fratino: 1959-2009. 50 anni di conservazione della biodiversità*. CFS/UTB Pratovecchio, Italy.
- Braun-Blanquet J., 1964. *Pflanzensoziologie. Grundzüge der Vegetationskunde* (3rd ed.). Springer, Wien.
- Brockerhoff, E.G., Barbaro, L., Castagneyrol, B., Forrester, D.I., Gardiner, B., González-Olabarria, J.R., Lyver, P.O., Meurisse, N., Oxbrough, A., Taki, H., Thompson, I.D., van der Plas, F., Jactel, H., 2017. Forest biodiversity, ecosystem functioning and the provision of ecosystem services. *Biodiversity and Conservation* 3005–3035. <https://doi.org/10.1007/s10531-017-1453-2>
- Brown, A.G., Hatton, J., Selby, K.A., Leng, M.J., Christie, N., 2013. Multi-proxy study of Holocene environmental change and human activity in the Central Apennine Mountains, Italy. *Journal of Quaternary Science* 28, 71–82. <https://doi.org/10.1002/jqs.2591>
- Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. *Ecological Bulletins* 53, 77–94. <https://doi.org/10.1016/j.jnc.2017.08.001>
- Burrascano, S., Chytrý, M., Kuemmerle, T., Giarrizzo, E., Luyssaert, S., Sabatini, F.M., Blasi, C., 2016. Current European policies are unlikely to jointly foster carbon sequestration and protect biodiversity. *Biological Conservation* 201, 370–376. <https://doi.org/10.1016/j.biocon.2016.08.005>
- Burrascano, S., Ripullone, F., Bernardo, L., Borghetti, M., Carli, E., Colangelo, M., Gangale, C., Gargano, D., Gentilella, T., Luzzi, G., Passalacqua, N., Pelle, L., Rivelli, A.R., Sabatini, F.M., Schettino, A., Siclari, A., Uzunov, D., Blasi, C., 2017. It's a long way to the top: Plant species diversity in the transition from managed to old-growth forests. *Journal of Vegetation Science* 98–109. <https://doi.org/10.1111/jvs.12588>
- Carli, E., Frondoni, R., Pinna, M.S., Bacchetta, G., Fenu, G., Fois, M., Marignani, M., Puddu, S., Blasi, C., 2018. Spatially assessing plant diversity for conservation: A Mediterranean case study. *Journal for Nature Conservation* 41, 35–43. <https://doi.org/10.1016/j.jnc.2017.11.003>
- Chiarucci, A., Bacaro, G., Scheiner, S.M., 2011. Old and new challenges in using species diversity for assessing biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences* 366, 2426–2437. <https://doi.org/10.1098/rstb.2011.0065>
- Chiarucci, A., Di Biase, R.M., Fattorini, L., Marcheselli, M., & Pisani, C., 2018. Joining the incompatible: Exploiting purposive lists for the sample-based estimation of species richness. *Annals of Applied Statistics*, 12, 1679–1699.
- Christensen, M., Heilmann-Clausen, J., 2009. Forest biodiversity gradients and the human impact in Annapurna Conservation Area, Nepal. *Biodiversity and Conservation*, 18, 2205–2221. <https://doi.org/10.1007/s10531-009-9583-9>
- Chytrý, M., 2001. Phytosociological data give biased estimates of species richness. *Journal of Vegetation Science* 12, 439–444. <https://doi.org/10.1111/j.1654-1103.2001.tb00190.x>
- Chytrý, M., Tichý, L., Hennekens, S.M., Schaminée, J.H.J., 2014. Assessing vegetation change using vegetation-plot databases: A risky business. *Applied Vegetation Science* 17, 32–41. <https://doi.org/10.1111/avsc.12050>
- Dengler, J., Jansen, F., Glöckler, F., Peet, R.K., de Cáceres, M., Chytrý, M., Ewald, J., Oldeland, J., Lopez-Gonzalez, G., Finckh, M., Mucina, L., Rodwell, J.S., Schaminée, J.H.J., Spencer, N., 2011. The Global Index of Vegetation-Plot Databases (GIVD): A new resource for vegetation science. *Journal of Vegetation Science* 22, 582–597. <https://doi.org/10.1111/j.1654-1103.2011.01265.x>
- Diekmann, M., Kühne, A., Isermann, M., 2007. Random vs non-random sampling: Effects on patterns of species abundance, species richness and vegetation-environment relationships. *Folia Geobotanica* 42, 179–190. <https://doi.org/10.1007/BF02893884>
- Díaz, S., Fargione, J., Chapin, F.S., Tilman, D., 2006. Biodiversity loss threatens human well-being. *PLoS Biology* 4, 1300–1305. <https://doi.org/10.1371/journal.pbio.0040277>
- FAO, 2018. *Global Forest Resources Assessment 2020. Terms and Definitions*.

<http://www.fao.org/3/I8661EN/i8661en.pdf> (accessed 8 January 2019)

- FAO, EFI, 2015. *State of Europe's Forests 2015*. <https://doi.org/10.2800/99473>
- Flensted, K.K., Bruun, H.H., Ejrnaes, R., Eskildsen, A., Thomsen, P.F., Heilmann-Clausen, J., 2016. Red-listed species and forest continuity - A multi-taxon approach to conservation in temperate forests. *Forest Ecology and Management* 378, 144–159. <https://doi.org/10.1016/j.foreco.2016.07.029>
- Gattone, S. A., Giordani, P., Di Battista, T., & Fortuna, F. (2018). Adaptive cluster double sampling with post stratification with application to an epiphytic lichen community. *Environmental and Ecological Statistics* 25, 125–138. <https://doi.org/10.1007/s10651-017-0388-9>
- Harrison, P.A., Berry, P.M., Simpson, G., Haslett, J.R., Blicharska, M., Bucur, M., Dunford, R., Egoh, B., Garcia-Llorente, M., Geamăna, N., Geertsema, W., Lommelen, E., Meiresonne, L., Turkelboom, F., 2014. Linkages between biodiversity attributes and ecosystem services: A systematic review. *Ecosystem Services* 9, 191–203. <https://doi.org/10.1016/j.ecoser.2014.05.006>
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., Connor, M.I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–108. <https://doi.org/10.1038/nature11118>
- Jansen, F., Glöckler, F., Chytrý, M., De Cáceres, M., Ewald, J., Finckh, M., Lopez-Gonzalez, G., Oldeland, J., Peet, R.K., Schaminée, J.H.J., Dengler, J., 2012. News from the Global Index of Vegetation-Plot Databases (GIVD): the metadata platform, available data, and their properties. *Biodiversity & Ecology* 4, 77–82. <https://doi.org/10.7809/b-e.00061>
- Jepsen, M.R., Kuemmerle, T., Müller, D., Erb, K., Verburg, P.H., Haberl, H., Vesterager, J.P., Andrič, M., Antrop, M., Austrheim, G., Björn, I., Bondeau, A., Bürgi, M., Bryson, J., Caspar, G., Cassar, L.F., Conrad, E., Chromý, P., Daugirdas, V., Van Eetvelde, V., Elena-Rosselló, R., Gimmi, U., Izakovicova, Z., Jančák, V., Jansson, U., Kladnik, D., Kozak, J., Konkoly-Gyuró, E., Krausmann, F., Mander, Ü., McDonagh, J., Pärn, J., Niedertscheider, M., Nikodemus, O., Ostapowicz, K., Pérez-Soba, M., Pinto-Correia, T., Ribokas, G., Rounsevell, M., Schistou, D., Schmit, C., Terkenli, T.S., Tretvik, A.M., Trzepak, P., Vadineanu, A., Walz, A., Zhllima, E., Reenberg, A., 2015. Transitions in European land-management regimes between 1800 and 2010. *Land use policy* 49, 53–64. <https://doi.org/10.1016/j.landusepol.2015.07.003>
- Kapfer, J., Hédl, R., Jurasinski, G., Kopecký, M., Schei, F.H., Grytnes, J.A., 2017. Resurveying historical vegetation data – opportunities and challenges. *Applied Vegetation Science* 20, 164–171. <https://doi.org/10.1111/avsc.12269>
- Kaufmann, S., Hauck, M., Leuschner, C., 2017. Comparing the plant diversity of paired beech primeval and production forests: Management reduces cryptogam, but not vascular plant species richness. *Forest Ecology and Management* 400, 58–67. <https://doi.org/10.1016/j.foreco.2017.05.043>
- Kraus, D., Krumm, F., 2013. *Integrative approaches as an opportunity for the conservation of forest biodiversity*, European Forest Institute.
- Kulakowski, D., Seidl, R., Holeksa, J., Kuuluvainen, T., Nagel, T.A., Panayotov, M., Svoboda, M., Thorn, S., Vacchiano, G., Whitlock, C., Wohlgemuth, T., Bebi, P., 2017. A walk on the wild side: Disturbance dynamics and the conservation and management of European mountain forest ecosystems. *Forest Ecology and Management* 388, 120–131. <https://doi.org/10.1016/j.foreco.2016.07.037>
- Lájer, K., 2007. Statistical tests as inappropriate tools for data analysis performed on non-random samples of plant communities. *Folia Geobot.* 42, 115–122. <https://doi.org/10.1007/BF02893878>
- Lengyel, S., Déri, E., Varga, Z., Horváth, R., Tóthmérész, B., Henry, P.Y., Kobler, A., Kutnar, L., Babij, V., Seliškar, A., Christia, C., Papastergiadou, E., Gruber, B., Henle, K., 2008. Habitat monitoring in Europe: A description of current practices. *Biodiversity and Conservation* 17, 3327–3339. <https://doi.org/10.1007/s10531-008-9395-3>
- Lepš, J., 2007. Subjectively sampled vegetation data: Don't throw out the baby with the bath water. *Folia Geobotanica* 42, 169–178. <https://doi.org/10.1007/BF02893883>
- Mölder, A., Streit, M., Schmidt, W., 2014. When beech strikes back: How strict nature conservation reduces herb-layer diversity and productivity in Central European deciduous forests. *Forest Ecology and Management* 319, 51–61. <https://doi.org/10.1016/j.foreco.2014.01.049>
- Müllerová, J., Hédl, R., Szabó, P., 2015. Coppice abandonment and its implications for species diversity in forest vegetation. *Forest Ecology and Management* 343, 88–100. <https://doi.org/10.1016/j.foreco.2015.02.003>
- Mori, A.S., Lertzman, K.P., Gustafsson, L., 2017. Biodiversity and ecosystem services in forest ecosystems: a research agenda for applied forest ecology. *Journal of Applied Ecology* 54, 12–27. <https://doi.org/10.1111/1365-2664.12669>
- Nascimbene, J., Dainese, M., Sitzia, T., 2013. Contrasting responses of epiphytic and dead wood-dwelling lichen diversity to forest management abandonment in silver fir mature woodlands. *Forest Ecology and Management* 289, 325–332. DOI: 10.1016/j.foreco.2012.10.052
- Paillet, Y., Bergès, L., Hjaltén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.T., Schmidt, W., Standovár, T., Tothmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conservation Biology* 24, 101–112. <https://doi.org/10.1111/j.1523-1739.2009.01399.x>
- Palmer, M.W., Earls, P.G., Hoagland, B.W., White, P. S., & Wohlgemuth, T., 2002. Quantitative tools for perfecting

- species lists. *Environmetrics*, 13, 121–138. <https://doi.org/10.1002/env.516>
- R Core Team, 2017. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Roberts, M. R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany* 82, 1273–1283. <https://doi.org/10.1139/b04-091>
- Roleček, J., Chytrý, M., Hájek, M., Lvončík, S., Tichý, L., 2007. Sampling design in large-scale vegetation studies: Do not sacrifice ecological thinking to statistical purism! *Folia Geobotanica* 42, 199–208. <https://doi.org/10.1007/BF02893886>
- Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Duarte, I.M., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O.-P., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2018. Where are Europe’s last primary forests? *Diversity and Distribution* 1–14. <https://doi.org/10.1111/ddi.12778>
- Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Schulze, E.D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T., Ammer, C., 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology* 55, 267–278. <https://doi.org/10.1111/1365-2664.12950>
- Scolastri, A., Cancellieri, L., Iocchi, M., Cutini, M., 2016. Old Coppice vs High Forest: the impact of beech forest management on plant species diversity in central Apennines (Italy). *Journal of Plant Ecology* 1–10. <https://doi.org/10.1093/jpe/rtw034>
- Scolastri, A., Bricca, A., Cancellieri, L., Cutini, M., 2017. Understorey functional response to different management strategies in Mediterranean beech forests (central Apennines, Italy). *Forest Ecology and Management* 400, 665–676. <https://doi.org/10.1016/j.foreco.2017.06.049>
- Sitzia, T., Campagnaro, T., Gatti, E., Sommacal, M., Kotze, D.J., 2015. Wildlife conservation through forestry abandonment: Responses of beetle communities to habitat change in the Eastern Alps. *European Journal of Forest Research* 134, 511–524. <https://doi.org/10.1007/s10342-015-0868-0>
- Spake, R., Ezard, T.H.G., Martin, P.A., Newton, A.C., Doncaster, C.P., 2015. A meta-analysis of functional group responses to forest recovery outside of the tropics. *Conservation Biology* 29, 1695–1703. <https://doi.org/10.1111/cobi.12548>
- Vacchiano, G., Garbarino, M., Lingua, E., Motta, R., 2017. Forest dynamics and disturbance regimes in the Italian Apennines. *Forest Ecology and Management* 388, 57–66. <https://doi.org/10.1016/j.foreco.2016.10.033>
- Vandekerckhove K., Thomaes A., Jonsson B.-G., 2013. Connectivity and fragmentation: island biogeography and metapopulation applied to old-growth elements. In: Kraus, D., Krumm, F., 2013. *Integrative approaches as an opportunity for the conservation of forest biodiversity*, European Forest Institute.
- Viciani, D., Gonnelli, V., Sirotti, M., Agostini, N., 2010. An annotated check-list of the vascular flora of the “Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna” (Northern Apennines Central Italy). *Webbia* 65, 3–131. <https://doi.org/10.1080/00837792.2010.10670867>
- Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A., McAlpine, C., Potapov, P., Walston, J., Robinson, J.G., Painter, M., Wilkie, D., Filardi, C., Laurance, W.F., Houghton, R.A., Maxwell, S., Grantham, H., Samper, C., Wang, S., Laestadius, L., Runting, R.K., Silva-Chávez, G.A., Ervin, J., Lindenmayer, D., 2018. The exceptional value of intact forest ecosystems. *Nature Ecology and Evolution* 2, 599–610. <https://doi.org/10.1038/s41559-018-0490-x>
- Zangheri, P., 1966. Flora e vegetazione del medio ed alto appennino romagnolo. *Webbia* 21, 1–450. <https://doi.org/10.1080/00837792.1966.10669838>

CHAPTER I

Are available vegetation data suitable for assessing plant diversity?

A study case in the Foreste Casentinesi National Park (Italy)

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ABSTRACT

This paper aimed to analyze potentials and shortcomings of existing vegetation data collected in an Italian National Park (Foreste Casentinesi NP) to: 1) assess coarse scale patterns of species diversity, and 2) set up a habitat monitoring system.

We generated a specifically designed georeferenced data set by assembling all available forest vegetation data, and then we analyzed spatial and temporal patterns of data by sample based accumulation and rarefaction curves. The analyses were performed on data gathered from the year 1934 to 2007. This broad temporal range may provide valuable information about processes occurring over a longer period than the majority of the published resurvey studies.

Our study revealed an uneven distribution of the records both in time and space, corroborating the view that this type of data is inappropriate to analyze trends of plant diversity at coarse scale. However, especially the oldest records of the data set represent a valuable source of information about long-term plant diversity changes, if used in resurvey studies designed with proper techniques. Detecting the directions of vegetation, or habitat, dynamics is crucial for addressing effective conservation actions.

Keywords: Forests, Phytosociological relevés, Plant diversity assessment, Vegetation resurvey.

<i>Contents</i>	<i>page</i>
1 Introduction	19
2 Materials and methods	20
2.1 Study area	20
2.2 Data assembly	21
2.3 Data analysis	22
3 Results	22
4 Discussion	25
5 Conclusions	27
Aknowledgements	27
References	27
Appendix 1	29

1 Introduction

In order to enhance nature conservation we firstly need to be informed on the status and trends of biodiversity. Accordingly, member States of European Union are required to report on status and changes of habitats listed in the Habitat Directive (92/43/EEC), mainly identified on the basis of vegetation types as described in the phytosociological literature (European Commission 2013). The long tradition of collecting vegetation data, according to the phytosociological approach (Braun-Blanquet 1964, Dengler 2017), has led to cumulate a huge amount of data (i.e. phytosociological relevés) at the plot scale (Chytrý et al. 2014). Globally, millions of them are already stored in electronic databases, with a special focus on many European countries (Dengler et al. 2011). Thus, these data potentially represent an important source of information for addressing several ecological questions. In particular, historical vegetation data might represent a tool for i) monitoring habitat dynamics, through resurvey studies, that are increasingly used for investigating changes in plant species diversity and composition (Kopecký and Macek 2015, Kapfer et al. 2017), and for ii) assessing patterns of plant diversity at multiple spatial scales, like at the scale of a whole protected area or even a larger region.

Nevertheless, the reliability and scientifically sound use of these data for quantitative purposes might be weakened by some intrinsic flaws that have to be taken into account in order to avoid misleading interpretations (Chytrý 2001, Chytrý and Otýpková 2003, Chiarucci 2007, Dengler 2009). In particular, we highlight here three critical issues: 1) the uncertainty of plots location with the risk of pseudo-turnover (Chytrý et al. 2014, Kopecký and Macek 2015, Alfonsi et al. 2017), i.e. a measured change in species composition not due to actual temporal variations but to a different spatial position of formerly and newly recorded plots; 2) the uneven temporal distribution of vegetation data (Haveman and Janssen 2008, Landucci et al. 2012), with most of them collected after the year 1970 (Dengler et al. 2011); 3) the preferential sampling approach adopted by phytosociologists, with the plots placed subjectively in “typical” stands considered representative of a given vegetation type (Chiarucci 2007, Roleček et al. 2007).

In this framework, we analyzed the suitability of phytosociological data collected over a long period for i) assessing spatial patterns of species diversity, and ii) setting up a habitat monitoring system at the scale of a protected area. As case study, we focused on a National Park (Foreste Casentinesi NP, Italy) mostly characterized by semi-natural forest habitats. In Italy, areas currently included in protected sites traditionally received great attention by botanists. Therefore, especially for these areas a large amount of information might be retrieved, in the form of floristic records and phytosociological relevés. Moreover, biodiversity assessment and habitat monitoring represent central activities for planning and evaluating conservation practices (e.g. Landi and Chiarucci 2014,

Pechanec et al. 2018). In this perspective, this study case may provide an early reference to develop a science-soundly use of available vegetation data for assessing plant diversity and for habitat monitoring in protected areas.

2 Materials and methods

2.1 Study area

The Foreste Casentinesi National Park ($43^{\circ}51'35.3''\text{N}$; $11^{\circ}45'32.2''\text{E}$) extends over an area of about $368,43 \text{ km}^2$, stretching across the ridge of the northern Apennines from 400 m a.s.l. to 1657 m a.s.l. (*Figure 1*). Along the elevational gradient, the annual mean temperature is between 8°C and 15°C , with average precipitation between 630 mm and 1900 mm per year (Antolini et al. 2017).

The protected area is mainly characterized by four geological formations: most of the Tuscan side is formed of “Macigno” sandstone, the Chianti sandstone (siliceous sandstone with low percentages of limestone), and the Mugello sandstone (silty schists with lower levels of marl and fine siliceous and calcareous sandstone). In the south-eastern Tuscan portion of the Park, the “Alberese” limestone emerges above a chaotic series of clayey rocks. The Romagna side is dominated by sandstone-marly flysch formations (Carta Geologica d’Italia 1969a, b).

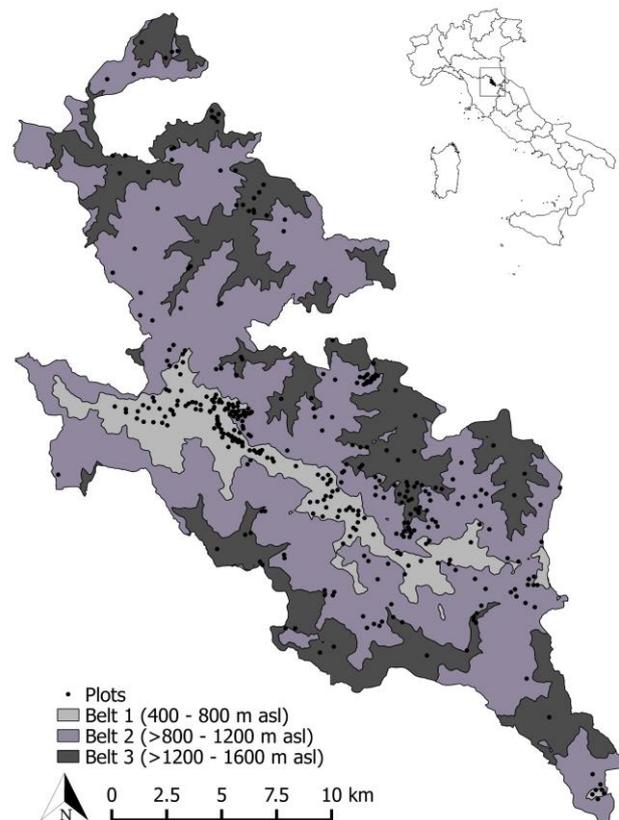


Figure 1 Map of the study area, the Foreste Casentinesi National Park, located in the northern Apennine (Italy) between the two administrative regions of Emilia-Romagna (north-east ridge of the Apennines chain) and Tuscany (south-west ridge).

This park is a core area for protecting and studying forest habitats. Almost 85% of its surface is covered by forests, in a system characterized by high forest connectivity and continuity, important features to permit the persistence of specialized forest species (Nordén et al. 2014). The forests in the park have a different degree of naturalness, including also the Integral Wildlife Reserve of Sasso Fratino Unesco Heritage. The beech forests (*Fagus sylvatica* L.) and the mixed broadleaf forests (with *Quercus cerris* L., *Quercus pubescens* Willd., *Ostrya carpinifolia* Scop., *Fraxinus ornus* L. etc.) are the dominant forest types, followed by coniferous plantations (mainly with *Abies alba* Mill. and *Pinus nigra* J.F. Arnold), chestnut (*Castanea sativa* Mill.) and mixed riparian forests (Viciani and Agostini 2008) (*Table 1*).

Table 1 Forest types described in the vegetation map of the Foreste Casentinesi National Park. In the third column the correspondence of the forest types with Natura 2000 habitats is reported. Natura 2000 habitats are indicated according to the standard codes used in the Annex 1 of the Habitat Directive (92/43/EEC).

Code	Forest type	Natura 2000 code
1	Beech forests (superior mountain belt)	9110, 9130, 9180*, 9210*, 9220*
2	Beech forests (inferior mountain belt)	9110, 9130, 9180*, 9210*, 9220*
3	Seminatural fir forests	9220*
4	Submountainous/hilly mesophilous forests (Romagna side)	9180*
5	Submountainous/hilly mesophilous forests (Tuscan side)	91L0
6	Submountainous/hilly xerophilous forests	
7	Seminatural chestnut forests	9260
8	Cultivated chestnut forests	
9	Coniferous plantations	
10	Riparian forests	91E0*, 92A0

2.2 Data assembly

We built a digital and georeferenced data set (*Appendix 1*) on the basis of available vegetation data. These data were retrieved both from published and unpublished sources and were included in the data set according to four criteria: 1) unambiguous location of the plot within the park; 2) accurate indication of site location (Haveman and Janssen 2008); 3) vegetation data surely referring to a forest community; 4) unambiguous indication of recording date.

Concerning the site location, we included in the data set only data with i) information about elevation, slope, aspect, locality name (that was the case, in our study, of data collected before the year 1970), ii) topographical maps (data from the year 1970 to the 2001, scale 1:25.000 or 1:50.000), or iii) spatial coordinates recorded by GPS devices (data after the year 2001).

Vegetation data were digitized and georeferenced (geographical reference system UTM WGS 84 zone 32 N) and added to the web geo-database VegItaly, based on the open source project anArchive for Botanical Data (Landucci et al. 2012). We carried out a homogenization of

taxonomic nomenclature by merging synonyms, removing taxa identified at the genus level, and aggregating subspecies at the species level (Conti et al. 2005).

2.3 Data analysis

To investigate the temporal pattern of knowledge accumulation targeted on the forest vegetation, we constructed a sample-based accumulation curve using the chronological ordering of samples (Gotelli and Colwell 2001, Fattorini 2013). In addition, we calculated also the accumulation of plot data along the temporal range to investigate the accumulation of sampling effort.

With the purpose to analyze species accumulation as function of sampling effort across forest types we built separate sample-based rarefaction curves (Gotelli and Colwell 2001, Fattorini 2013). We stratified the forest areas into types according to the park vegetation map (Viciani and Agostini 2008) then we calculated separate rarefaction curves for each type.

Sample-based accumulation and rarefaction curves were built by means of the function “specaccum()” in the “vegan” R package (Oksanen 2016), using the methods “collector” (for accumulation curves) and “exact” (for rarefaction curves). The “collector” method provided the cumulative number of species, by pooling the samples in the order they were recorded. The “exact” method provided the means of repeated re-sampling of all pooled samples (Gotelli and Colwell 2001) using a formula that has been independently developed numerous times (Chiarucci et al. 2008), often referred to Mao Tau estimate (Colwell et al. 2012).

We analysed the distribution of vegetation data in relation to the forest types and along the elevational gradient, stratified into three belts ranging 400 m, by means of Pearson's Chi-squared tests (R “stats” package). All the analyses were performed with R software version 3.2.3 (R Core Team, 2016) and QGIS software version 2.12 (QGIS Development Team 2016).

3 Results

A total of 386 vegetation plot data, were retrieved and selected to be stored in the database. These data were collected between the years 1934 and 2007. Overall, 450 vascular plant species were recorded.

The collection of vegetation data within the study area started very early, but proceeded slowly until the year 1970, with a marked increase of sampling effort after this period. Accordingly, the cumulative number of species detected for the park reflected the temporal pattern of survey effort (*Figure 2*).

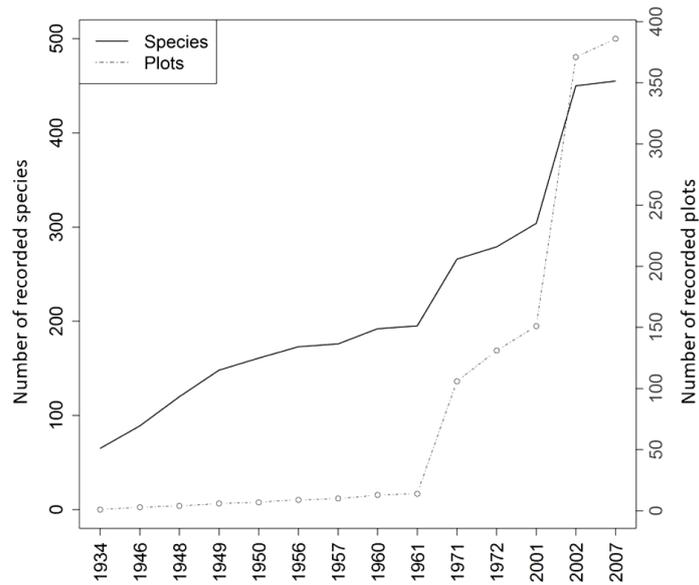


Figure 2 Temporal pattern of forest vegetation data included in the georeferenced data set (Foreste Casentinesi National Park). Sample-based accumulation curves represent the single order of samples (recorded plots) and species (recorded species) successively pooled in the time-series (ranging between the years 1934 and 2007).

Concerning the spatial patterns, the sampling effort was uneven and largely focused on the upper elevational belt, between 1200 m a.s.l. and 1600 m a.s.l. (Figure 3), with wide areas, especially at the mid and low elevations, almost lacking data.

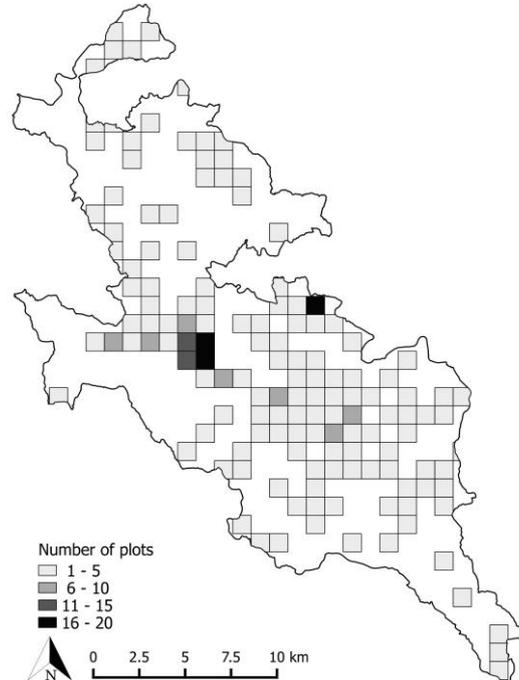


Figure 3 Sampling effort (number of forest vegetation data included in the georeferenced data set ranging from the year 1934 to 2007) for grid cell (1 km x 1 km) in the Foreste Casentinesi National Park. Only cells containing data are shown.

Accordingly, the actual and estimated number of vegetation data, in relation to the surface of each belt, showed significant differences (*Table 2*).

Table 2 Results of the Pearson's Chi-squared tests performed between the actual and the estimated number of samples, calculated considering the relative surface of each elevational belt and forest type in the study area. In both the cases differences are significant.

	Value	df	p-value
Elevational belts	75.189	2	< 2.2e-16
Forest types	111.5	9	< 2.2e-16

The upper belt (up to 1200 m a.s.l.) was oversampled, while the intermediate belt (800 m a.s.l. - 1200 m a.s.l.) and the lower belt (400 m a.s.l. - 800 m a.s.l.) were under sampled (*Table 3*). The majority of data collected before the year 2000 was mainly concentrated above 1200 m a.s.l. (59% of the data until the year 1961 and 47% of the data between the years 1971 and 2000), while most of the data after the year 2000 were sampled at an elevation between 800 m a.s.l. and 1200 m a.s.l. (43% of the data after the year 2000).

Table 3 Actual and estimated number of samples for elevational belt considering the relative area of each belt. The belts were obtained by splitting the study area into three elevational areas ranging 400 m. The symbol * indicates the oversampled belt.

Belt	Range	Area %	Actual	Estimate
1	400-800	35	82	134
2	> 800-1200	54	157	208
*3	> 1200-1650	11	147	44

Differences were significant also considering the distribution of data across forest types (*Table 2*), with most of the vegetation data sampled in beech forests (types 1, 2 in the *Table 1*) across the whole time range (86% of samples before the year 1961, 53% of the samples between the years 1971 and 2000, 44% of the samples after the year 2000); 38% of the vegetation plots in the intermediate period (1971-2000) were sampled in fir forests (type 3 in the *Table 1*), while 37% of the plots after the year 2000 were sampled in mixed broadleaf forests (types 4, 5, 6 in the *Table 1*). Accordingly, comparing the sample-based rarefaction curves (*Figure 4*), near-saturation of species numbers occurred only for beech, fir forests, and the mixed broadleaf forests.

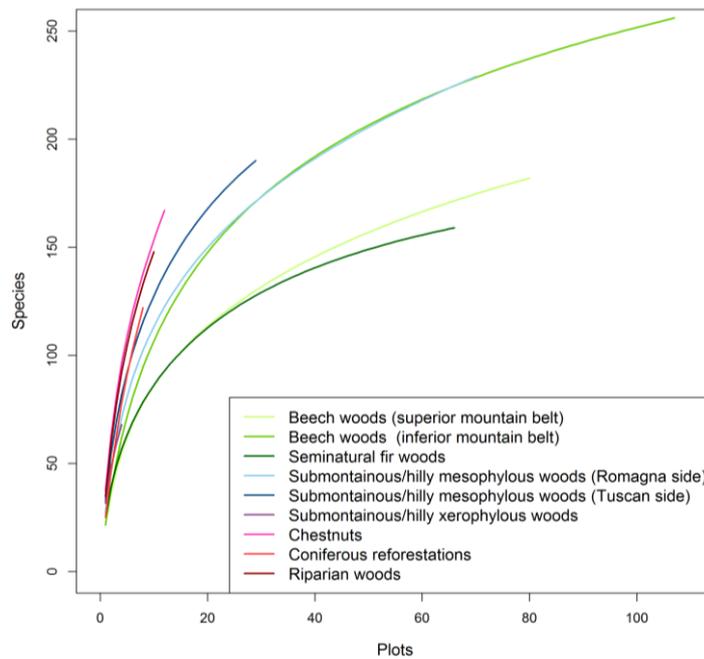


Figure 4 Sample-based rarefaction curves of species detected in each forest type: 1) Beech forests (superior mountain belt); 2) Beech forests (inferior mountain belt); 3) Seminatural fir forests; 4) Submontainous/hilly mesophilous forests (Romagna side); 5) Submontainous/hilly mesophilous forests (Tuscan side); 6) Submontainous/hilly xerophilous forests; 7) Seminatural chestnut forests; 8) Cultivated chestnut forests; 9) Coniferous plantations; 10) Riparian forests. We aggregated the similar types (7) and (8) due to only one sample for the latter type.

The distance from saturation did not depend on the number of samples placed in relation to the size of each forest type (*Table 4*).

Table 4 Actual and estimated number of samples for forest type considering the relative area of each type in the study area. The symbol * indicates oversampled forest types.

Forest type	Forest area %	Actual	Estimate
Beech forests (superior mountain belt)*	4.4	80	17
Beech forests (inferior mountain belt)	35.7	107	138
Seminatural fir forests*	6.2	66	24
Submontainous/hilly mesophilous forests (Romagna side)	20.9	70	81
Submontainous/hilly mesophilous forests (Tuscan side)	10.7	29	41
Submontainous/hilly xerophilous forests	2.0	4	8
Seminatural chestnut forests	3.5	11	14
Cultivated chestnut forests	1.0	1	4
Coniferous plantations	14.9	8	57
Riparian forests*	0.7	10	3

4 Discussion

In this research, we aimed to analyze the suitability of phytosociological data collected over a long period for i) assessing spatial patterns of species diversity, and ii) setting up a habitat monitoring system at the scale of a protected area. Our findings corroborate the view that the use of this data type for monitoring and conservation planning should carefully consider the uncertainty in plot

location and the uneven temporal-spatial distribution of information. While the use of these data for describing the habitat types and their species composition may be scientifically sound, their suitability for assessing spatial and temporal patterns of plant diversity is controversial, potentially leading to misleading interpretations (Roleček et al. 2007, Chytrý et al. 2014, Kapfer et al. 2017). The results for an intensively sampled area, as it is the case of the Foreste Casentinesi NP, support the cautionary approach of using existing phytosociological data for analyzing such of spatial and temporal patterns.

The uncertainty in plot location associated to the data analyzed in this work might affect results of resurveys aimed at monitoring habitat dynamics and vegetation shifts over time. Indeed, spatial uncertainty might lead to biased conclusions in relocation studies where pseudo-turnover occurs (Kapfer et al. 2017). As possible solutions to overcome this problem, researchers proposed data stratifications (e.g. Haveman and Janssen 2008, Kopecký and Macek, 2015, Alfonsi et al. 2017, Kapfer et al. 2017) or to replicate samples spatially close to the best estimate of the formerly surveyed historical plot (Ross et al. 2010, Chytrý et al. 2014). Therefore, filtering past data for spatial accuracy and applying methods that take into account the uncertainty in location, the resurvey of vegetation data may represent a suitable tool for investigating the effects of habitat changes on plant species assemblages (Fauth et al. 1996). For this target, the data set we built and analyzed in this work has a high potential to inform on long-time changes. In fact, we digitized vegetation data since the 1930s (Zangheri 1966), much older than most of the data already stored in electronic databases (Dengler et al. 2011). Thus, the relocation of these ancient data with proper methods may provide valuable information from a broader temporal perspective than the majority of the resurvey studies (Kapfer et al. 2017).

Concerning the assessment of plant diversity patterns, our results indicate that the uneven temporal and spatial distribution of sampling effort may represent a relevant pitfall intrinsically contained in phytosociological data accumulated over the years in a given area without a specific sampling design, and this can likely lead to biased conclusions. In fact, differences in sampling intensity across the time range were consistent also with the variation in the number of recorded species (i.e. increasing the sampling effort the number of recorded plant species increased even independently to actual vegetation changes). However, we are aware that the uneven temporal distribution of data may be also linked with one of the criteria followed for including the vegetation data in the georeferenced database that is the availability of information to spatially locate each vegetation record. Indeed, data recorded far back in time are likely to have been excluded in a higher proportion simply because of the lack of spatial information.

In addition to the temporal pattern, also the uneven distribution of phytosociological relevés across forest types and along the elevational gradient is consistent with a typical process of the botanical

accumulation of data (Palmer et al. 2002), that makes rather difficult to properly infer about spatial patterns of species composition or diversity (Lájer 2007, Chiarucci 2007, Palmer et al. 2008). Consequently, the use of data collected with such preferential methods should not be adopted for analyzing spatial patterns of plant diversity at the landscape and/or regional level and for making inference about the spatial patterns of species richness and composition (Diekmann et al. 2007, Haveman and Janssen 2008).

5 Conclusions

Three main conclusions can be drawn from our study case:

- 1) Retrieving and analysing vegetation data sampled until now may help to identify knowledge gaps (both in the space and in relation to different habitat types) towards which moving further research efforts;
- 2) With appropriate stratified sampling methods, the resurvey of historical vegetation data may represent a useful source of information about vegetation and habitat changes. In particular, the oldest data presented in this work, dating back to the decade 1930s, have a high potential for informing about long-term vegetation shifts;
- 3) Vegetation data collected according to the phytosociological approach seems to be inappropriate to infer patterns of plant diversity, due to pitfalls associated to the uneven temporal and spatial distribution of the data. For this target, a probabilistic approach, in particular a stratified random sampling, might be more suitable (Diekmann et al. 2007).

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References

- Alfonsi E, Benot M-L, Fievet V, Alard D (2017) Addressing species turnover and community changes in vegetation resurvey studies. *Appl Veg Sci* 20:172–182. <https://doi.org/10.1111/avsc.12258>
- Antolini G, Pavan V, Tomozeiu R, Marletto V (2017) Atlante climatico dell'Emilia-Romagna 1961-2015. Arpae E-R. <https://www.arpae.it> (accessed 5 February 2018).
- Braun-Blanquet J (1964) *Pflanzensoziologie. Grundzüge der Vegetationskunde*, 3rd edn. Springer, Wien
- Carta Geologica d'Italia (1969a) Foglio 107, Monte Falterona, scala 1:100.000. Litografia Artistica Cartografica, Firenze

- Carta Geologica d'Italia (1969b) Foglio 108, Mercato Saraceno, scala 1:100.000. Litografia Artistica Cartografica, Firenze
- Chiarucci A (2007) To sample or not to sample? That is the question... For the vegetation scientist. *Folia Geobot* 42:209–216. <https://doi.org/10.1007/BF02893887>
- Chiarucci A, Bacaro G, Rocchini D, Fattorini L (2008) Discovering and rediscovering the sample-based rarefaction formula in the ecological literature. *Community Ecol* 9:121–123. <https://doi.org/10.1556/ComEc.9.2008.1.14>
- Chytrý M (2001) Phytosociological data give biased estimates of species richness. *J Veg Sci*, 12:439–444. <https://doi.org/10.1111/j.1654-1103.2001.tb00190.x>
- Chytrý M, Otýpková Z (2003) Plot sizes used for phytosociological sampling of European vegetation. *J Veg Sci* 14:563–570. <https://doi.org/10.1111/j.1654-1103.2003.tb02183.x>
- Chytrý M, Tichý L, Hennekens SM, Schaminée JHJ (2014) Assessing vegetation change using vegetation-plot databases: A risky business. *Appl Veg Sci* 17:32–41. <https://doi.org/10.1111/avsc.12050>
- Colwell RK, Chao A, Gotelli NJ, Lin SY, Mao CX, Chazdon RL, Longino JT (2012). Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. *J Plant Ecol* 5:3–21. <https://doi.org/10.1093/jpe/rtr044>
- Conti F, Abbate G, Alessandrini A and Blasi C (ed) (2005). An annotated checklist of the Italian vascular flora. Palombi, Rome
- Dengler J (2009). A flexible multi-scale approach for standardised recording of plant species richness patterns. *Ecol Indic* 9:1169–1178. <https://doi.org/10.1016/j.ecolind.2009.02.002>
- Dengler J et al. (2011) The Global Index of Vegetation-Plot Databases (GIVD): A new resource for vegetation science. *J Veg Sci* 22:582–597. <https://doi.org/10.1111/j.1654-1103.2011.01265.x>
- Dengler J (2017) Phytosociology. In Richardson D, Castree N, Goodchild MF, Kobayshi AL, Liu W, Marston R (ed) *The international encyclopedia of geography: people, the Earth, environment, and technology*. Wiley-Blackwell, Chichester
- Diekmann M, Kühne A, Isermann M (2007) Random vs non-random sampling: effects on patterns of species abundance, species richness and vegetation-environment relationships. *Folia Geobot* 42:179–190. <https://doi.org/10.1007/BF02893884>
- European Commission (2013) Interpretation Manual of European Union Habitats. EUR28, Brussels
- Fattorini S (2013) Regional insect inventories require long time, extensive spatial sampling and good will. *PLoS ONE* 8. <https://doi.org/10.1371/journal.pone.0062118>
- Fauth J E, Bernardo J, Camara M, Resetarits WJ, Buskirk Jr, Van Buskirk J, McCollum SA (1996) Simplifying the Jargon of Community Ecology : A Conceptual Approach. *Am Soc Nat* 147:282–286. <https://doi.org/10.1086/285850>
- Gotelli NJ, Colwell RK (2001) Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecol Lett* 43:379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>
- Haveman R, Janssen JAM (2008) The analysis of long-term changes in plant communities using large databases: the effect of stratified resampling. *J Veg Sci* 19:355–362. <https://doi.org/10.3170/2008-8-18375>
- Kapfer J, Hédli R, Jurasinski G, Kopecký M, Schei FH, Grytnes J-A (2017) Resurveying historical vegetation data – opportunities and challenges. *Appl Veg Sci* 20:164–171. <https://doi.org/10.1111/avsc.12269>
- Kopecký M, Macek M (2015) Vegetation resurvey is robust to plot location uncertainty. *Divers Distrib* 21:322–330. <https://doi.org/10.1111/ddi.12299>
- Lájer K (2007) Statistical tests as inappropriate tools for data analysis performed on non-random samples of plant communities. *Folia Geobot* 42:115–122. <https://doi.org/10.1007/BF02893878>
- Landi S, Chiarucci A (2014) Commonness and rarity of plants in a reserve network: just two faces of the same coin. *Rend Lincei* 25:369–380. <https://doi.org/10.1007/s12210-014-0313-1>
- Landucci F, Acosta ATR, Agrillo E, Attorre F et al. (2012) VegItaly: the Italian collaborative project for a national vegetation database. *Plant Biosyst* 146:756–763. <https://doi.org/10.1080/11263504.2012.740093>
- Nordén B, Dahlberg A, Brandrud TE, Fritz Ö, Ejrnaes R, Ovaskainen O (2014) Effects of ecological continuity on species richness and composition in forests and woodlands: a review. *Écoscience* 21:34–45. <https://doi.org/10.2980/21-1-3667>
- Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2016) *Vegan : ecological diversity*. R package version 2.4–2. URL: <https://cran.r-project.org/web/packages/vegan/index.html>. Accessed on 5 February 2018
- Palmer MW, Earls PG, Hoagland BW, White PS, Wohlgemuth T (2002) Quantitative tools for perfecting species lists. *Environmetr* 13:121–137. <https://doi.org/10.1002/env.516>

- Palmer MW, McGlenn DJ, Fridley JD (2008) Artifacts and artificions in biodiversity research. *Folia Geobot* 43:245–257. <https://doi.org/10.1007/s12224-008-9012-y>
- Pechanec V et al. (2018) Effectiveness of Natura 2000 system for habitat types protection: a case study from the Czech Republic. *Nat Conserv* 24:21–41. DOI: 10.3897/natureconservation.24.21608
- QGIS Development Team (2016) QGIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org> (accessed 5 February 2018).
- R Core Team (2017) R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/> (accessed 5 February 2018).
- Roleček J, Chytrý M, Hájek M, Lvončík S, Tichý L (2007) Sampling design in large-scale vegetation studies: Do not sacrifice ecological thinking to statistical purism! *Folia Geobot* 42:199–208. <https://doi.org/10.1007/BF02893886>
- Ross LC, Woodin SJ, Hester A, Thompson DBA, Birks HJB (2010) How important is plot relocation accuracy when interpreting re-visitation studies of vegetation change? *Plant Ecol Divers* 3:1–8. <https://doi.org/10.1080/17550871003706233>
- Viciani D, Agostini N (2008) La carta della vegetazione del Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna (Appennino Tosco-Romagnolo): note illustrative. *Quad Stud Nat Studi Nat Romagna* 27:97–134
- Zangheri P (1966) Flora e vegetazione del medio e alto Appennino Romagnolo vol.5. In: Zangheri P (ed) *Romagna Fitogeografica*. Forni, Sala Bolognese, pp 1-451. <https://doi.org/10.1080/00837792.1966.10669838>

Appendix 1

Sources of vegetation data included in the georeferenced data set. For each reference the number of recorded samples and the associated spatial information are reported, as well as the year of sampling.

Plots	Reference	Year of sampling	Field personnel	Spatial information
14	Zangheri P (1966) Flora e vegetazione del medio e alto Appennino Romagnolo vol.5. In: Zangheri P (ed) <i>Romagna Fitogeografica</i> . Forni, Sala Bolognese, pp 1-451	1934-1961	Zangheri P.	toponym, elevation, aspect, slope
22	Bentivogli D (1971-1972) Ricerche fitosociologiche sui cedui di faggio al Passo della Calla. Degree thesis, Supervisor Prof. Augusto Pirola, University of Bologna, Italy. Unpubl.	1971	Bentivogli D., Pirola A.	topographic map (1:25.000), elevation, aspect, slope
25	Senzani G (1971-1972) Appartenenza fitosociologica del bosco ad Abies alba di Campigna. Degree thesis, Supervisor Prof. Augusto Pirola, University of Bologna, Italy. Unpubl.	1971	Senzani G., Pirola A.	topographic map (1:25.000), elevation, aspect, slope
45	Schirinzi S (1971-1972) Aggruppamenti floristici e fitosociologici del bosco della Lama (Forlì). Degree thesis, Supervisor Prof. Augusto Pirola, University of Bologna, Italy. Unpubl.	1971	Schirinzi S., Pirola A.	topographic map (1:25.000), elevation, aspect
25	Monti E (1972-1973) Determinazione della struttura dell'Abieti-Fagetum di Campigna (Appennino Romagnolo). Degree thesis, Supervisor Prof. Augusto Pirola, University of Bologna, Italy. Unpubl.	1972	Monti E., Pirola A.	topographic map (1:25.000), elevation, aspect, slope
20	Salvatori L (2001-2002) Tipologia e dinamica della vegetazione nel biotopo di Capria (Santa Sofia -FC). Degree thesis, Supervisor Prof. Giovanna Puppi, University of Bologna, Italy. Unpubl.	2001	Salvatori L., Puppi G.	topographic map (1:50.000), elevation, aspect, slope
220	Viciani D, Agostini N (2008) La carta della vegetazione del Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna (Appennino Tosco-Romagnolo): note illustrative. <i>Quad Stud Nat Studi Nat Romagna</i> 27:97–134.	2002	Fariselli R., Gabellini A., Sirotti M., Viciani D.	topographic map (1:25.000) and GPS coordinates, elevation, aspect, slope
15	Table of samplings. Unpubl.	2007	Gabellini A.	GPS coordinates, elevation, aspect, slope

CHAPTER II

Comparing preferential and probabilistic surveys to assess and monitor plant diversity in Protected Areas

Chapter to be published as:

Lelli, C.¹, Nascimbene, J.¹, Chiarucci, A.¹, Comparing preferential and probabilistic surveys to assess and monitor plant diversity in Protected Areas.

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ABSTRACT

Question: Can preferential and probabilistic surveys provide comparable information for assessing and monitoring plant diversity within protected areas?

Location: Foreste Casentinesi National Park, Italy

Methods: We compared two vegetation surveys performed in the same study area according to two different approaches: 1) a preferential survey of vegetation data collected according to the phytosociological approach; 2) a probabilistic survey of vegetation data sampled according to a spatial stratified sampling. We compared the performance of the two surveys focusing on (i) topographical and (ii) ecological information (i.e., beta diversity, rarity/commonness of sampled species, habitat species groups).

Results: Topography was differently represented by the two survey methods, due to a different spatial distribution of plots within the study area. In terms of species composition, both samplings covered about the same vegetation variability. Despite this overlap in species composition, the preferential survey resulted more focused on recording habitat specialist species, as compared to the probabilistic survey, which caught more intermediate situations.

Conclusions: The probabilistic survey provides a statistically representative picture of plant communities, but may fail in the detection of some biodiversity features that are spatially localized and important for assessing the conservation status of species and habitats. Therefore, the integration between a systematic probabilistic survey with an expert-based selection of sites of particular interest and/or rarity, could improve the cost-effectiveness of monitoring plant diversity in protected areas.

Key-words: Complementarity, Forests, Habitat specialist species, Monitoring, Phytosociological survey, Sampling design, Stratified-random survey, Vegetation.

<i>Contents</i>	<i>page</i>
1 Introduction	32
2 Materials and methods	33
2.1 Study area	33
2.2 Data collection	34
2.2.1 Preferential survey	35
2.2.2 Probabilistic survey	35
2.3 Data analysis	35
3 Results	36
4 Discussion	39
Aknowledgements	42
References	42

1 Introduction

Protected areas are currently considered the cornerstones of conservation strategies (e.g., Gallardo et al., 2017). Europe has one of the largest coordinated networks of protected areas in the world, including the Natura 2000 network of protected sites (EEA, <http://www.eea.europa.eu/>), coupled with national-level protected areas (i.e., reserves and national parks) (Gallardo et al., 2017; UNEP-WCMC, www.protectedplanet.net). However, despite recent international projects (e.g., EuMon project, <http://eumon.ckff.si>) and policies (e.g. EU Habitat Directive [92/43/EEC](#)), the availability of data on the status and trends of biodiversity in protected areas is still unbalanced across countries. This problem is mainly related to the lack of data systematically collected according to quantitative and comparable methods (Gaston et al., 2006; Chiarucci, Bacaro, and Rocchini, 2008; Chiarucci et al., 2012), most of survey schemes being planned at the local level (Lengyel et al., 2008). This is also reflected by weak national and international data sharing, as indicated for example by the absence of many South-Eastern European Countries from GBIF intergovernmental initiative for open access to biodiversity data (GBIF, <https://www.gbif.org/>). This situation determines gaps in fundamental information that should be available for planning effective biodiversity conservation (Gaston et al., 2006), urgently claiming for the development of standardized monitoring approaches across Europe (e.g., Bacaro, Baragatti, and Chiarucci, 2009; Chiarucci, Bacaro, and Scheiner, 2011).

For vascular plants, there is a long history of research on the topic of sampling design in vegetation science, but the lagging implementation in monitoring systems is still weakening their effectiveness (e.g., Lepš, 2007; Roleček, Chytrý, Hájek, Lvončík, and Tichý, 2007; Lengyel et al., 2008). Sampling methods can be grouped into one of two categories: preferential (i.e., sampling sites are chosen based on the subjective decision of the researcher) and probabilistic sampling (i.e., the selection of sampling sites is completely independent from the researcher) (Swacha, Botta-Dukát, and Kački, 2017). On one hand, preferential sampling, based on the phytosociological method (Braun-Blanquet, 1964), has provided a huge amount of vegetation data across decades and is still widely used (Jansen et al., 2012). This method, based on maximizing across plots heterogeneity and within plot homogeneity for identifying and sampling “typical” vegetation units, is mainly adopted for documenting the diversity of vegetation types, according to a-priori recognition of discrete vegetation units, and for monitoring vegetation and habitat changes over time (Chytrý, Tichý, Hennekens, and Schaminée, 2014). Nevertheless, it has intrinsic methodological pitfalls mainly related to the subjectivity in placing the sampling plots which may bias statistical and quantitative inferences (e.g., Lájér, 2007; Chiarucci, 2007; Lelli, Nascimbene, and Chiarucci, 2018). On the other hand, probabilistic survey may overcome these flaws, allowing a more consistent assessment

of plant diversity (e.g., Roleček et al., 2007), since it is based on a statistically representative location of sampling units, by using random schemes or stratification criteria to improve sampling efficiency (e.g., Grabherr, Reiter, and Willner, 2003). However, despite the fact that the probabilistic survey method could be more appropriate for monitoring plant diversity, it has been argued that it may fail in recording rare species and assemblages (Diekmann, Kühne, and Isermann, 2007; Roleček et al., 2007).

Further, different sampling methods may produce divergent results regarding species diversity patterns (Swacha, Botta-Dukát, and Kački, 2017), potentially leading to misleading conclusions for conservation. Long-term nature conservation needs effective tools to face the increasing impacts which are affecting ecosystems at multiple temporal and spatial scales (UNEP–WCMC, <http://www.biodiversitya-z.org>; Pereira et al., 2010). In this context, properly designed surveys provide the baseline for monitoring patterns and trends of biodiversity that is fundamental for identifying priorities in conservation planning (Kovač, Kutnar, and Hladnik, 2016; Xu et al., 2017; Carli et al., 2018).

With this study, we directly compared the performance of the preferential vs. probabilistic sampling methods within a major protected area in Italy, the Foreste Casentinesi National Park (FCNP), with the purpose to summarize their main properties, by evaluating their relative divergence and their suitability for the assessment and monitoring of plant diversity. Specifically, we analyzed their performance in terms of recording data (1) well-distributed according to the topographic variability of the study area, since topography may play a relevant role in shaping plant communities (Janssen et al., 2018), and (2) representative of the variability of plant communities within the study area.

2 Materials and methods

2.1 Study area

The FCNP (43°51'35.3"N; 11°45'32.2"E) extends over an area of about 368,43 km², stretching across the ridge of the northern Apennines from 400 m a.s.l. to 1657 m a.s.l., in the regions of Emilia Romagna and Tuscany (*Figure 1*).

The mean annual temperature is 10°C, ranging between 13°C and 7°C along the elevational gradient; the mean annual rainfall is 1388 mm, ranging from 1082 mm to 1612 mm. Climatic data refer to the period 1991-2015 for Emilia-Romagna and 1995-2014 for Tuscany.

The two main geological formations are the sandstones, arenaceous marls unit (Middle-lower Miocene) in the Romagna side and the Sandstones, arenaceous marls unit (sometimes turbiditic; Paleogene) in the Tuscan side with limestones and clays unit (turbiditic; Palaeogene) along the Apennine ridge (Geoportale Nazionale).

Forests cover almost 85% of the FCNP surface with different degrees of naturalness, ranging from the Integral Reserve of Sasso Fratino Unesco Heritage (Bottacci, 2009) to intensively managed stands (i.e., coppices and high forests). At higher elevation (up to 900-1000 m a.s.l.) beech forests (*Fagus sylvatica* L.) dominate, in pure and mixed formations with *Acer pseudoplatanus* L. and *Abies alba* Mill., while at lower and intermediate elevation mixed broadleaf formations prevail, including oaks (*Quercus cerris* L., and *Q. pubescens* Willd.), chestnuts (*Castanea sativa* Mill.), hop hornbeams (*Ostrya carpinifolia* Scop.), and the Italian maple (*Acer opalus* Mill.). Conifer plantations cover almost 15% of the FCNP, mostly composed of silver fir (*Abies alba* Mill.) and black pines (*Pinus nigra* J.F. Arnold.). Pure chestnut (*Castanea sativa*) formations, as well as riparian forests dominated by common alder (*Alnus glutinosa* (L.) Gaertn.) are rare (Viciani and Agostini, 2008; Viciani, Gonnelli, Sirotti, and Agostini, 2010).

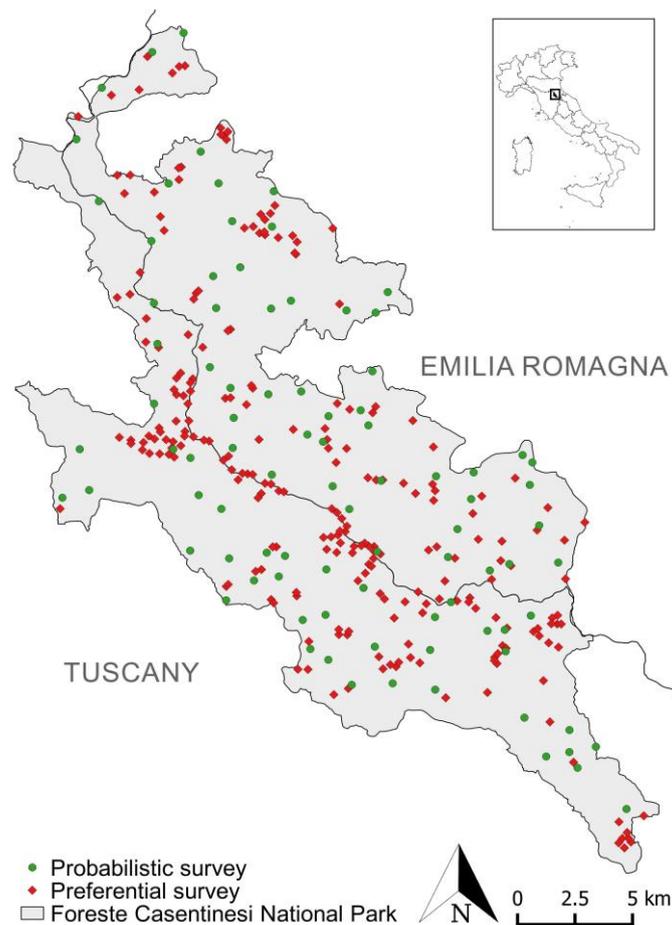


Figure 1 Location of the study area, the Foreste Casentinesi National Park, Italy (FCNP).

2.2 Data collection

In this comparative study, we used data collected by two different vegetation surveys within the FCNP: the first data set was retrieved from a previous preferential survey carried out by using the phytosociological approach; the second data set was obtained by a specifically performed probabilistic survey. Both data sets are related only to forests, that dominate the landscape of the

FCNP, and included species co-occurrence information (i.e., a complete list of plant species within each plot), as well as plot-based environmental data. The nomenclature of the species was unified according to Conti, Abbate, Alessandrini, and Blasi (2005).

2.2.1 Preferential survey

The preferential survey (PREF) consisted of plots sampled during summer 2002 by four experienced botanists (Viciani and Agostini, 2008). Field work was carried out according to the phytosociological approach (Braun-Blanquet, 1964). Vegetation plots were located with expert-based assessment aimed at covering the variability of the vegetation types in the study area, by minimizing the within-plot heterogeneity, with a previous stratification in vegetation types based on photointerpretation of remote-sensing images, further checked by expert-based field evaluation. Plots differed in size (ranging from 100 to 400 m²) following the concept of minimal area, i.e. the smallest area that contains the species of regular occurrence within a stand (Otypková and Chytrý, 2006). Of the whole data set, including 400 plot-data, we considered in this study 289 plot-data sampled within forests. We removed also those plots located outside the boundaries of the FCNP or lacking accurate spatial references, with a final data set of 235 plots.

2.2.2 Probabilistic survey

In summer (May-July) 2016 and 2017, we carried out a field survey based on a probabilistic sampling design (PROB). Survey points were spatially stratified in order to avoid clusters (Økland, 2007): a regular grid of 1 km x 1 km cells was overlaid to the FCNP area and one random point was extracted within each cell. We used the FCNP vegetation map (Viciani and Agostini, 2008) to binary stratify forested vs. non-forested areas. Only points within forested areas were selected, resulting in a potential pool of 317 points. Considering the cost-effectiveness constrains, we selected a subset of 90 points according to a stratification based on the elevational gradient of the FCNP (i.e., splitting the forested areas in three elevation belts equally spanning 400 m) to keep a balanced spatial distribution of the survey. Each point was located with a GPS device (Garmin Oregon 450t) and a squared plot of 10 m x 10 m was surveyed. Three plots were further excluded from the analyses due to recent forestry practices therein (e.g., Grabherr et al., 2003).

2.3 Data analysis

We compared the two sampling methods in terms of topographical (elevation, slope) and ecological (species habitat groups, common/rare species, beta-diversity) information.

In order to standardize the size of the two data sets, with 87 probabilistic plots vs. 325 preferential plots, we randomly extracted from the preferential data set 1000 replicates of 87-plot subsamples, without replacement within each set.

Topographical data were derived by a Digital Elevation Model (DEM) with 20 m of spatial accuracy. We compared elevations and slopes of the probabilistic data set vs. the 1000 preferential subsamples using the Wilcoxon signed rank test. With the same statistical test, we analyzed also the topographical differences between the data sets and the topography of the whole study area, that was obtained by extrapolating elevation and slopes for cells of 20 m x 20 m (from the DEM) covering the whole park surface.

To compare the species composition recorded by the probabilistic survey and the preferential subsamples, we calculated beta diversity (function “beta.pair”, betapart R package, Baselga et al., 2018) using the Jaccard dissimilarity index on presence/absence data, between each preferential subsample and the probabilistic data set. We performed Principal Coordinate Analysis (PCoA) (function “betadisper”, betapart R package) to visualize differences in species composition between the two methods and applied ANOVA to test for significant differences.

Then, we classified the species into groups according to their habitat affiliation (e.g., Amici et al., 2015): (1) “forest species” (F), i.e. species exclusive of forest habitats, (2) “non-forest species” (N), i.e. species specialized for open habitats, including wood margins, and (3) “generalist species” (G), i.e. species which can grow in a wide range of habitats, both forests and open habitats (Pignatti, 1982, Viciani et al., 2010). We compared the surveys in terms of habitat groups and common/rare species, by ranking the species according to their relative frequency of occurrence in each data set (i.e., the probabilistic data set and the 1000 preferential subsamples) (McGeoch and Gaston, 2002), defining as “rare species” those occurring in less than five plots (from 1 to 5 plots), and “common species” those species occurring in more than 40 plots (from 40 to 87 plots). We calculated the percentage of common and rare F, N, G species for the probabilistic data set and the preferential subsamples of common/rare species.

All the analyses were performed using R software version 3.2.3 (R Core Team, 2017) and QGIS software version 2.12 (QGIS Development Team, 2016).

3 Results

A total of 325 species was recorded by the probabilistic survey, while 370 species were recorded by the preferential survey.

Topography was differently represented by the methods, due to a different spatial distribution of plots within the study area. Distribution of probabilistic and preferential plots along the elevational gradient of the study area differed, with an overrepresentation of high elevations in the preferential subsamples. Indeed, elevations of the probabilistic data set were significantly different (p -value < 0.05) and lower than the preferential subsamples in 985 tests out of 1000 (98.5%). Elevations of the 94.3% of preferential subsamples were also significantly different and greater than

the distribution of elevations of the whole study area (PNFC) (*Figure 2*). Probabilistic plots caught higher slopes as compared to the preferential subsamples, with a significant difference in 621 out of 1000 tests (62.1%). Slopes of the 26% of preferential subsamples were also significantly different, and lower, than the slopes of the whole study area (PNFC) (*Figure 2*).

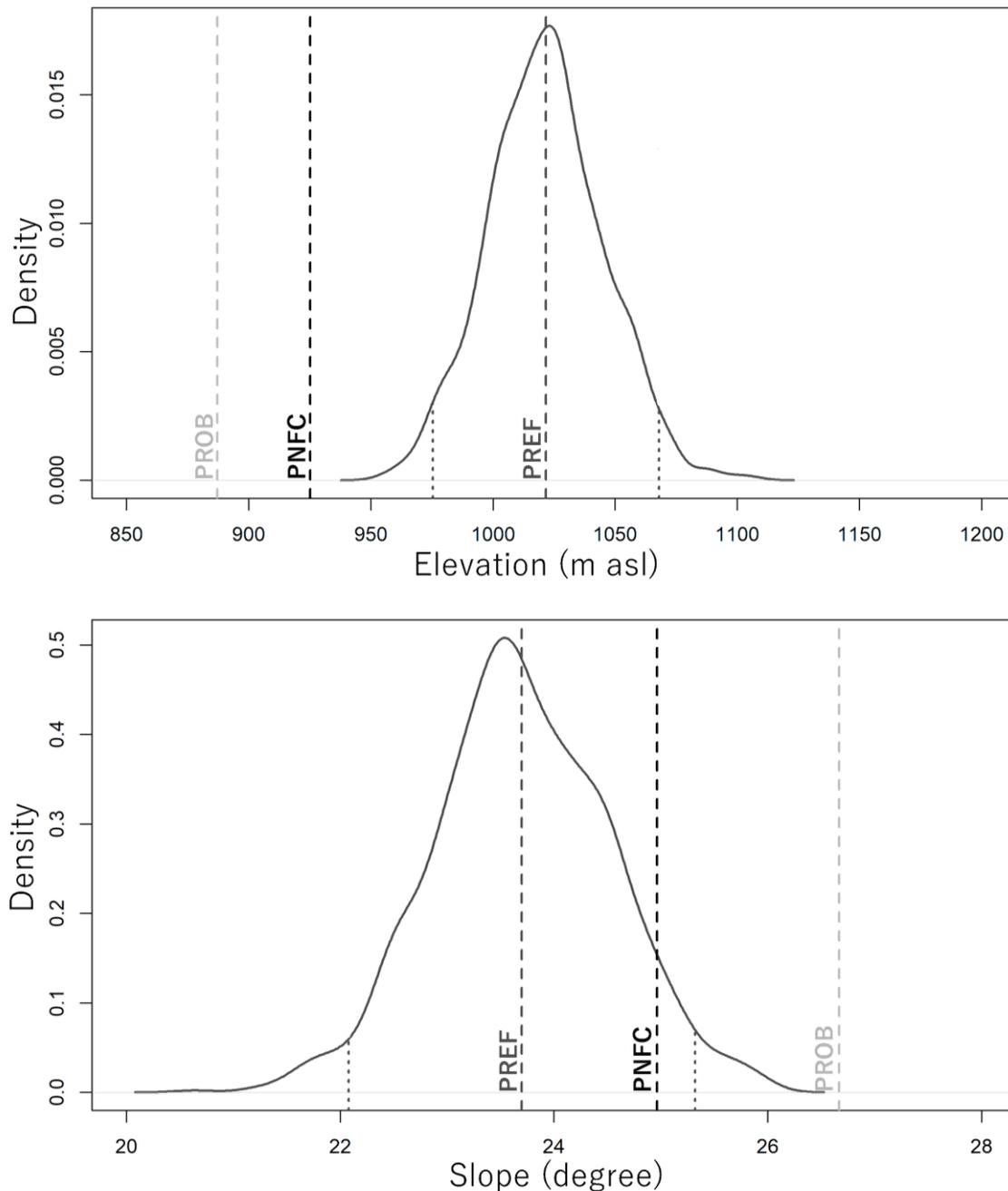


Figure 2 Kernel density plot of the mean elevations (above) and slopes (below) of the 1000 subsets randomly extracted from the preferential data set. The y-axis represents the probability density function for the kernel density estimation. Dotted lines are the 95% confidence intervals for the density distributions (i.e., 95% of the observations are included between the lines). ELEVATIONS: Dashed lines are the mean elevations of the preferential subsets (PREF, darkgrey: mean = 1021.6, SD = 23.6), the probabilistic data set (PROB, lightgrey: mean = 887.2, SD = 210.9) and the whole study area (PNFC, black: mean = 925.2, SD = 208.8).

SLOPES: Dashed lines are the mean slopes of the preferential subsets (PREF, darkgrey: mean = 23.7, SD = 0.8), the probabilistic data set (PROB, lightgrey: mean = 26.6, SD = 11.8) and the whole study area (PNFC, black: mean = 24.9, SD = 10.5).

The mean elevation and slope of the preferential subsets have been calculated by averaging the mean values of the 1000 replicates.

In terms of species composition, both methods covered about the same vegetation variability. Beta diversity was significantly different between the probabilistic data set and each of the 1000 preferential subsets for the 20% of the comparisons. In *Figure 3* four out of the 1000 comparisons are shown. Despite this overlap in species composition, we evidenced some notable differences considering common and rare species recorded by the two methods (*Figure 4*). Indeed, the preferential method caught a higher percentage of forest-specialist species (F), both considering the rare and the common species. On the contrary, a higher amount of non-forest (N) and generalist species (G) was recorded by the probabilistic survey, especially considering the rare species (*Figure 4*).

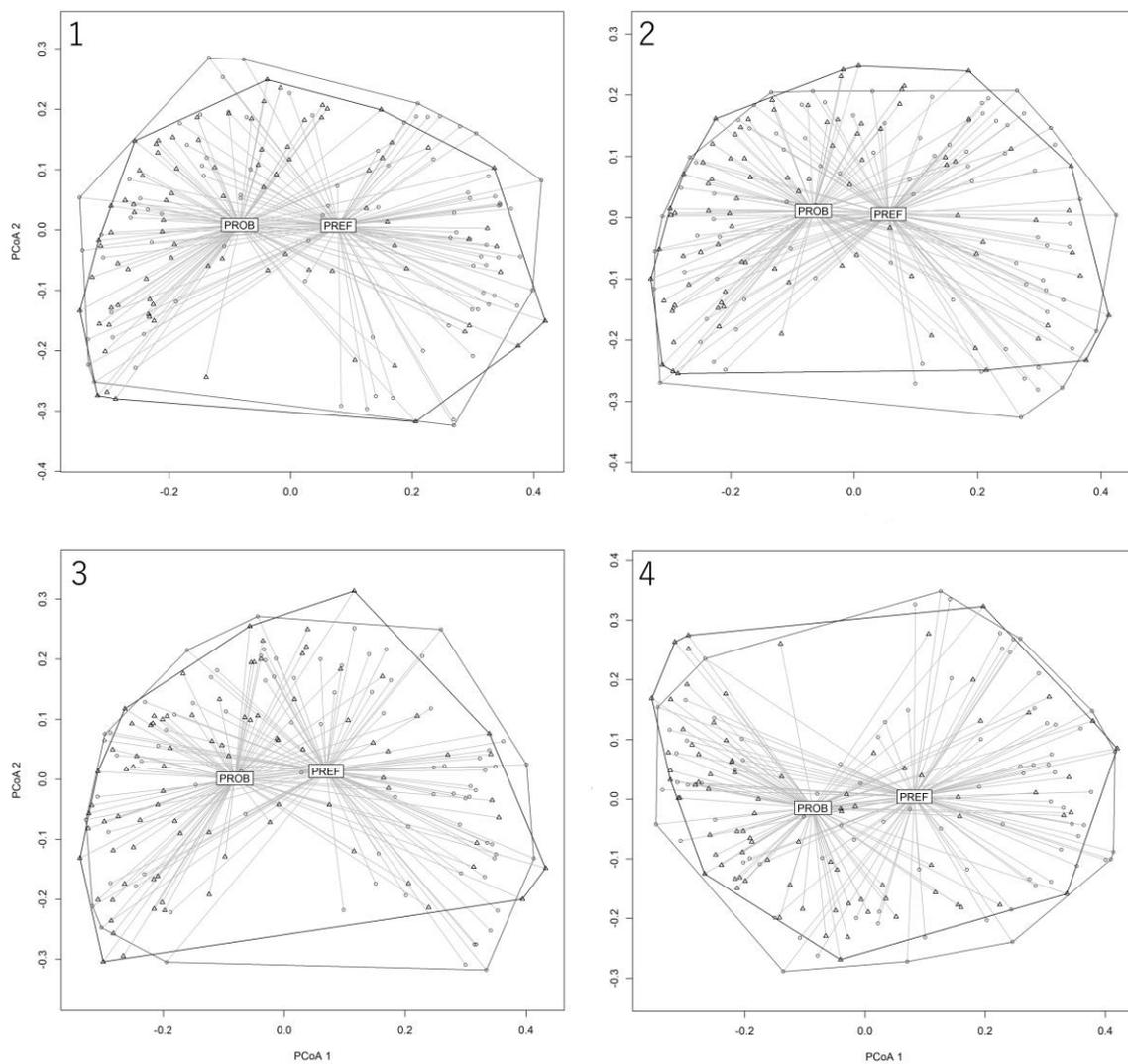


Figure 3 Beta diversity: the PCoA plots show an overlap between the species composition of the probabilistic (PROB) and the preferential (PREF) data sets. Triangles are PROB plots, circles are PREF plots. Here four out of the 1000 comparisons, between the PROB data set and the PREF subsamples are shown.

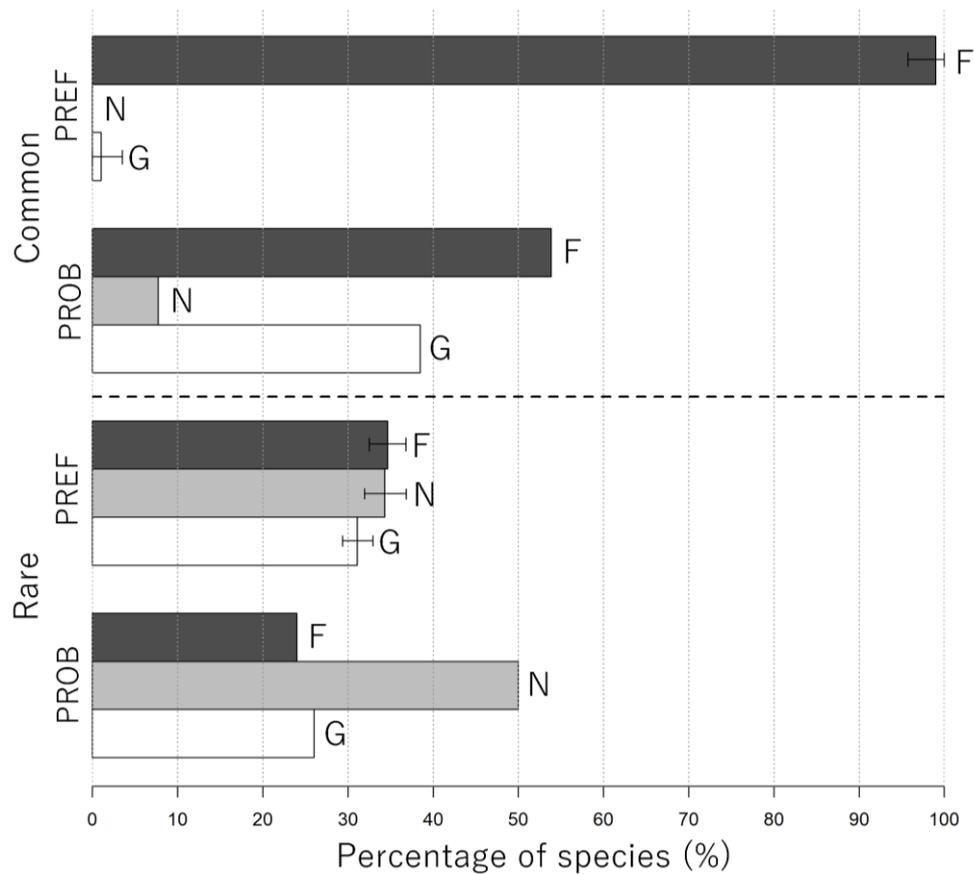


Figure 4 Rare/Common species comparison between the probabilistic (PROB) data set and the preferential (PREF) subsamples. Species are divided into habitat groups (F: forest species, N: Non forest species, G: Generalist species). Rare species occurred in less than five plots (from 1 to 5 plots). Common species occurred in more than 40 plots (from 40 to 87 plots). For the preferential subsamples we averaged the percentages obtained by all the 1000 samples (bars represent the standard deviations of the means).

4 Discussion

Our comparative study on the performance of preferential vs. probabilistic sampling methods for plant diversity evidenced that contrasting properties of these two methods produce different results and ecological interpretations. However, these divergences may be considered as complements and both sources of information could be integrated to maximize the effectiveness of plant diversity assessment and monitoring in protected areas.

To be effective, a sampling method should ensure the collection of reliable data for statistical processing and ecological inference (Swacha, Botta-Dukát, and Kącki, 2017).

In these terms, on the one hand, a probabilistic method may guarantee standardization for an unbiased replicability that is fundamental for monitoring activities (Hill, Fasham, Tucker, Shewry, and Shaw, 2005) and can permit statistically sound comparisons of temporal trends (Yoccoz, Nichols, and Boulinier, 2001; Ferretti and Chiarucci, 2003; Chiarucci et al., 2011). Further, a probabilistic survey based on a spatial and topographic stratification of samples, as in our study case, may guarantee a better representation of the study area, in terms both of topographical

attributes, and even, indirectly, of species diversity patterns. Indeed, topography may play a relevant role in shaping plant communities, especially on mountain systems, exacerbating differences even over small distances (Janssen et al., 2018). On the contrary, the subjective sampling of plots, according to the preferential method, could lead recording only a fraction of the topographic variability of the study area, with the risk of overestimating the occurrence of some plant species and assemblages, for instance overrepresenting high elevation forests while undersampling low elevation forests (Lelli, Nascimbene, and Chiarucci, 2018). Notwithstanding, the cons of an unbiased spatial distribution of plots, as in the case of the probabilistic survey, lies in the potential occurrence of plots even in remote or less accessible sites (e.g., at high slopes and roughness), thus requiring high sampling effort. Accordingly, Schreuder, Gregoire, and Weyer (1999), argued that much environmental data can only be collected using preferential surveys due to difficult sampling processes, access and safety issues, or time and expenses.

On the other hand, it has been emphasized that a probabilistic survey may fail in the detection of biodiversity features that are spatially localized and important for assessing the conservation status of species and habitats (e.g., Palmer et al. 2002; Chiarucci, 2007). In fact, probabilistic sampling methods result in the under-representation of rare vegetation types, rare species or habitat specialists, if the chosen sample size is not extensive enough, but a very high sampling intensity is impractical especially in studies at large spatial scales (Smartt and Grainger, 1974; Hédli, 2007). By contrast, the subjective approach at the base of the preferential sampling, not derived by some model or probability distribution, that has been described by Palmer, Earls, Hoagland, White, and Wohlgemuth (2002) as the “use of internal algorithms” by the experienced botanists, can cause bias in the data collection, as it is the case of the oversampling and undersampling of some parts of the ecological gradient (Lájer, 2007; Chiarucci, 2007), but it also likely outperforms any probabilistic methodology in maximizing the recording of rare species, assemblages, or habitat specialist species, such as those on localized situations or rare habitats (Palmer et al. 2002; Chiarucci, 2007). Therefore, the risk of the preferential sampling method is to produce biased conclusions about vegetation variability due to the intentional restriction of vegetation variation, i.e., focusing on “typical vegetation types”, as well as on more peculiar assemblages (Swacha, Botta-Dukát, and Kački, 2017), but it is also recognized as a more efficient method for finding rare vegetation types in the landscape, while probabilistic sampling predominantly records dominant community types and more intermediate situations (Smartt and Grainger, 1974; Chytrý, 2001; Botta-Dukát, Kovács-Láng, Rédei, Kertész, and Garadnai, 2007; Diekmann et al., 2007; Roleček et al., 2007; Swacha, Botta-Dukát, and Kački, 2017). In our study the two survey methods showed an overlap in the overall species composition recorded, that was probably due also to the stratification of the preferential sampling design by vegetation type from remote sensing images, which likely increased

the representativeness of the preferentially obtained sample. Despite this overall overlap, the preferential survey resulted actually more focused on forest specialist species, both considering rarely and frequently recorded species, as compared to the probabilistic survey that caught more intermediate/transitory situations, as indicated by the high percentage of non-forest species.

In summary, despite the statistical limitations inherent to the preferential survey (e.g., Palmer et al., 2002; Diekmann et al., 2007; Lájér, 2007), its effectiveness in providing insights on rare species or assemblages can be seen as a complement of a statistically more sound probabilistic survey, thus improving the cost-effectiveness of monitoring plant diversity. Therefore, the integration between a systematic probabilistic survey, with an expert-based selection of sites of particular interest and/or rarity, could maximize the sampling of species diversity within an area. The use of auxiliary information to improve estimation has a long standing in sample surveys and several recent attempts provided methodological implementation for possible approaches in biodiversity surveys (e.g., Speak, Escobedo, Russo, and Zerbe, 2018). For instance, Yih Lam, Hsu, Yang, Kershaw, and Su (2018) recently proposed a 3P sampling (probability proportional to prediction) with a sampling that integrate expert knowledge into a probabilistic design, allocating higher effort to areas with high species richness based on predictions made in the field. Further, Xu et al. (2017) proposed a large-monitoring scheme with an approach to allocate minimum monitoring sites to the most informative areas, based on species richness, diversity and complementarity. Another methodological improvement to the use of preferential data was provided by Chiarucci, Di Biase, Fattorini, Marcheselli, and Pisani (2018), who developed a new method that makes use of lists of species obtained by purposive (preferential) sampling to improve sample-based estimation of species richness. Finally, approaches to improve probabilistic sampling to record rare species assemblages have been developed, such as the possibility to include simple and easy to measure auxiliary variable in adaptive sampling, as done by the adaptive cluster double sampling (Félix-Medina and Thompson, 2004). This method has recently been used to detect rare lichen communities, by using a two-phase sampling process without requiring a-priori delineation of the strata, but estimating the strata sizes in the course of the sampling process (Gattone, Giordani, Di Battista, and Fortuna, 2018). This sophisticated approach is still largely lacking in vegetation and habitat monitoring, but the urgent need for quantitative and repeatable methods is really calling for a new phase of testing the pros and cons of various sampling approaches, as we did here, and the development of new methods such as those based on multi stage unequal probability sampling (see e.g., Tillé and Ecker, 2014).

In conclusion, our study corroborates the view that biodiversity assessment and monitoring carried out with different sampling designs can produce different pictures of biodiversity and that it is fundamental to attempt the requirements of probabilistic and standardized sampling methods which

can be integrated by expert knowledge. A good integration between different approaches might enhance the survey strategies targeted at monitoring plant diversity to achieve those sound data that are fundamental for biodiversity conservation.

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References

- Amici, V., Rocchini, D., Filibeck, G., Bacaro, G., Santi, E., Geri, F., ... Chiarucci, A., 2015. Landscape structure effects on forest plant diversity at local scale: Exploring the role of spatial extent. *Ecological Complexity*, 21, 44–52. <https://doi.org/10.1016/j.ecocom.2014.12.004>.
- Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Bacaro, G., Baragatti, E., & Chiarucci, A. (2009). Using taxonomic data to assess and monitor biodiversity: are the tribes still fighting? *Journal of Environmental Monitoring*, 11, 798. DOI: 10.1039/B818171N
- Baselga A., Orme, D., Villeger, De Bortoli, J., & Leprieur, F. (2018, February 22). Betapart: partitioning beta diversity into turnover and nestedness components. R package version 1.4-1. Retrieved from <https://CRAN.R-project.org/package=betapart>
- Botta-Dukát, Z., Kovács-Láng, E., Rédei, T., Kertész, M., & Garadnai, J. (2007). Statistical and biological consequences of preferential sampling in phytosociology: Theoretical considerations and a case study. *Folia Geobotanica*, 42, 141–152. <https://doi.org/10.1007/BF02893880>
- Bottacci A. (Ed.) (2009). La Riserva Naturale Integrale di Sasso Fratino: 1959-2009. 50 anni di conservazione della biodiversità. CFS/UTB Pratovecchio, Italy.
- Braun-Blanquet J. (1964). *Pflanzensoziologie. Grundzüge der Vegetationskunde* (3rd ed.). Springer, Wien. <https://doi.org/10.1007/978-3-7091-8110-2>
- Carli, E., Frondoni, R., Pinna, M.S., Bacchetta, G., Fenu, G., Fois, M., ... Blasi, C. (2018). Spatially assessing plant diversity for conservation: A Mediterranean case study. *Journal for Nature Conservation*, 41, 35–43. <https://doi.org/10.1016/j.jnc.2017.11.003>
- Chiarucci, A. (2007). To sample or not to sample? That is the question... For the vegetation scientist. *Folia Geobotanica*, 42, 209–216. <https://doi.org/10.1007/BF02893887>
- Chiarucci, A., Bacaro, G., & Rocchini, D. (2008). Quantifying plant species diversity in a Natura 2000 network: Old ideas and new proposals. *Biological Conservation*, 141, 2608–2618. <https://doi.org/10.1016/j.biocon.2008.07.024>
- Chiarucci, A., Bacaro, G. & Scheiner, S.M. (2011). Old and new challenges in using species diversity for assessing biodiversity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 2426–2437. <http://rstb.royalsocietypublishing.org/cgi/doi/10.1098/rstb.2011.0065>
- Chiarucci, A., Bacaro, G., Filibeck, G., Landi, S., Maccherini, S., & Scoppola, A. (2012). Scale dependence of plant species richness in a network of protected areas. *Biodiversity and Conservation*, 21, 503–516. <https://doi.org/10.1007/s10531-011-0196-8>
- Chiarucci, A., Di Biase, R.M., Fattorini, L., Marcheselli, M., & Pisani, C. (2018). Joining the incompatible: Exploiting purposive lists for the sample-based estimation of species richness. *Annals of Applied Statistics*, 12, 1679–1699.
- Chytrý, M. (2001). Phytosociological data give biased estimates of species richness. *Journal of Vegetation Science*, 12,

- 439–444. <https://doi.org/10.1111/j.1654-1103.2001.tb00190.x>
- Chytrý, M., Tichý, L., Hennekens, S.M., & Schaminée, J.H.J. (2014). Assessing vegetation change using vegetation-plot databases: A risky business. *Applied Vegetation Science*, 17, 32–41. <https://doi.org/10.1111/avsc.12050>
- Conti, F., Abbate G., Alessandrini, A., Blasi, C. (Eds.) (2005). An Annotated Checklist of the Italian Vascular Flora. Palombi, Rome.
- Diekmann, M., Kühne, A. & Isermann, M. (2007). Random vs non-random sampling: Effects on patterns of species abundance, species richness and vegetation-environment relationships. *Folia Geobotanica*, 42, 179–190. <https://doi.org/10.1007/BF02893884>
- EEA (2018, September 30). Retrieved from <https://www.eea.europa.eu>
- EuMon project (2018, September 30). Biodiversity monitoring in Europe. Retrieved from <http://eumon.ckff.si>.
- Félix-Medina, M., & Thompson, S. (2004). Adaptive cluster double sampling. *Biometrika*, 91, 877–891. <https://doi.org/10.1093/biomet/91.4.877>
- Ferretti, M., & Chiarucci, A. (2003). Design concepts adopted in long-term forest monitoring programs in Europe – problems for the future? *The Science of the Total Environment*, 310, 171–178. [https://doi.org/10.1016/S0048-9697\(02\)00637-X](https://doi.org/10.1016/S0048-9697(02)00637-X)
- Gallardo, B., Aldridge, D.C., González-Moreno, P., Pergl, J., Pizarro, M., Pyšek, P., ... Vilà, M. (2017). Protected areas offer refuge from invasive species spreading under climate change. *Global Change Biology*, 23, 5331–5343. <https://doi.org/10.1111/gcb.13798>
- Gaston, K.J., Charman, K., Jackson, S.F., Armsworth, P.R., Bonn, A., Briers, R.A., ... Tratt, R. (2006). The ecological effectiveness of protected areas: The United Kingdom. *Biological Conservation*, 132, 76–87. <https://doi.org/10.1016/j.biocon.2006.03.013>
- Gattone, S. A., Giordani, P., Di Battista, T., & Fortuna, F. (2018). Adaptive cluster double sampling with post stratification with application to an epiphytic lichen community. *Environmental and Ecological Statistics*, 25, 125–138. <https://doi.org/10.1007/s10651-017-0388-9>
- GBIF. Free and open access to biodiversity data. Retrieved from <https://www.gbif.org/the-gbif-network> (accessed 15 January 2019)
- Geoportale Nazionale. Carta geologica d'Italia alla scala 1:500.000 (2013). Retrieved from <http://www.pcn.minambiente.it> (accessed 15 January 2019)
- Grabherr, G., Reiter, K. & Willner, W. (2003). Towards objectivity in vegetation classification: The example of the Austrian forests. *Plant Ecology*, 169, 21–34. <https://doi.org/10.1023/A:1026280428467>
- Hédl R. (2007). Is sampling subjectivity a distorting factor in surveys for vegetation diversity? *Folia Geobotanica*, 42, 191–198. <https://doi.org/10.1007/BF02893885>
- Hill, D., Fasham, M., Tucker, G., Shewry, M., & Shaw, P. (Eds.) (2005). Hand-book of biodiversity-survey, evaluation and monitoring. Cambridge University Press, New York.
- Jansen, F., Glöckler, F., Chytrý, M., De Cáceres, M., Ewald, J., Finckh, M., ... Dengler, J. (2012). News from the Global Index of Vegetation-Plot Databases (GIVD): the metadata platform, available data, and their properties. *Biodiversity & Ecology*, 4, 77–82. DOI: 10.1111/j.1654-1103.2011.01265.x
- Janssen, P., Fuhr, M., & Bouget, C. (2018). Small variations in climate and soil conditions may have greater influence on multitaxon species occurrences than past and present human activities in temperate mountain forests. *Diversity and Distribution*, 1–14. <https://doi.org/10.1111/ddi.12705>
- Koleff, P., Gaston, K.J., & Lennon, J.J. (2003). Measuring beta diversity for presence-absence data. *Journal of Animal Ecology*, 72, 367–382. <https://doi.org/10.1046/j.1365-2656.2003.00710.x>
- Kovač, M., Kutnar, L., Hladnik, D. (2016) Assessing biodiversity and conservation status of the Natura 2000 forest habitat types: tools for designated forestlands stewardship. *Forest Ecology and Management*, 359, 256–267. <https://doi.org/10.1016/j.foreco.2015.10.011>
- Lájer, K. (2007). Statistical tests as inappropriate tools for data analysis performed on non-random samples of plant communities. *Folia Geobotanica*, 42, 115–122. <https://doi.org/10.1007/BF02893878>
- Lelli, C., Nascimbene, J., & Chiarucci, A. (2018). Are available vegetation data suitable for assessing plant diversity? A study case in the Foreste Casentinesi National Park (Italy). *Rendiconti Lincei Scienze Fisiche e Naturali*, 29, 355–362. <https://doi.org/10.1007/s12210-018-0681-z>
- Lengyel, S., Déri, E., Varga, Z., Horváth, R., Tóthmérész, B., Henry, P.Y., ... Henle, K. (2008). Habitat monitoring in Europe: A description of current practices. *Biodiversity and Conservation*, 17, 3327–3339.
- Lepš, J. (2007). Subjectively sampled vegetation data: Don't throw out the baby with the bath water. *Folia Geobotanica*, 42, 169–178. <https://doi.org/10.1007/s10531-008-9395-3>
- McGeoch, M. A., & Gaston, K. J. (2002). Occupancy frequency distributions: patterns, artefacts and mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, 77, S1464793101005887. <https://doi.org/10.1017/S1464793101005887>
- Økland, R.H. (2007). Wise use of statistical tools in ecological field studies. *Folia Geobotanica*, 42, 123–140. <https://doi.org/10.1007/BF02893879>
- Oksanen, J., Blanchet F. G., Friendly, M., Kindt, R., Legendre, P., McGlenn, D., ... Wagner, H. (2018, May 17). Vegan: community ecology package. Version 2.4-5. Retrieved from <https://cran.r-project.org/web/packages/vegan/index.html> (accessed 15 January 2019)
- Otypková, Z., & Chytrý, M. 2006. Effects of plot size on the ordination of vegetation samples. *Journal of Vegetation*

- Science*, 17, 465–472. <https://doi.org/10.1111/j.1654-1103.2006.tb02467.x>
- Palmer, M.W., Earls, P.G., Hoagland, B.W., White, P. S., & Wohlgemuth, T. (2002). Quantitative tools for perfecting species lists. *Environmetrics*, 13, 121–138. <https://doi.org/10.1002/env.516>
- Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., ... & Walpole, M. (2010). Scenarios for global biodiversity in the 21st century. *Science*, 330, 1496–1501. <https://doi.org/10.1126/science.1196624>
- Pignatti S. (1982). Flora d'Italia. Edagricole, Bologna.
- QGIS Development Team (2016). QGIS geographic information system. Open source geospatial foundation project. Retrieved from <http://qgis.osgeo.org> (accessed 15 January 2019)
- R Core Team (2017). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. Retrieved from <https://www.R-project.org/> (accessed 15 January 2019)
- Roleček, J., Chytrý, M., Hájek, M., Lvončík, S., & Tichý, L. (2007). Sampling design in large-scale vegetation studies: Do not sacrifice ecological thinking to statistical purism! *Folia Geobotanica*, 42, 199–208. <https://doi.org/10.1007/BF02893886>
- Schreuder, H. T., Gregoire, T. G., & Weyer, J. P. (1999). For what applications can probability and non- probability sampling be used? *Environmental Monitoring and Assessment*, 66, 281–91. <https://doi.org/10.1023/A:1006316418865>
- Smartt PFM, Grainger EA. (1974). Sampling for vegetation survey: some aspects of the behaviour of unrestricted, restricted, and stratified techniques. *Journal of Biogeography*, 1, 193–206. <https://doi.org/10.2307/3037969>
- Swacha, G., Botta-Dukát, Z., & Kački, Z. 2017. A performance comparison of sampling methods in the assessment of species composition patterns and environment – vegetation relationships in species-rich grasslands. *Acta Societatis Botanicorum Poloniae*, 86, 3561. <https://doi.org/10.5586/asbp.3561>
- Tillé, Y., & Ecker, K. (2014). Complex national sampling design for long-term monitoring of protected dry grasslands in Switzerland. *Environmental and Ecological Statistics*, 21, 453–476. <https://doi.org/10.1007/s10651-013-0263-2>
- UNEP-WCMC (2018, September 27). World Database of Protected Areas. Retrieved from www.protectedplanet.net
- UNEP-WCMC (2018, September 27). Biodiversity A-Z. Retrieved from <http://www.biodiversitya-z.org>
- Viciani, D., & Agostini, N. (2008). La carta della vegetazione del Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna (Appennino Tosco-Romagnolo): note illustrative. *Quaderno di Studi e Notizie di Storia Naturale della Romagna*, February, 97–134.
- Viciani, D., Gonnelli, V., Sirotti, M., & Agostini, N. (2010). An annotated check-list of the vascular flora of the “Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna” (Northern Apennines Central Italy). *Webbia*, 65, 3–131. <https://doi.org/10.1080/00837792.2010.10670867>
- Xu, H., Cao, M., Wu, Y., Cai, L., Cao, Y., Ding, H., ... & Li, J. (2017). Optimized monitoring sites for detection of biodiversity trends in China. *Biodiversity and Conservation*, 26, 1959–1971. <https://doi.org/10.1007/s10531-017-1339-3>
- Yih Lam, T., Hsu, Y.-H., Yang, T.-R., Kershaw, J.A., & Su, S.-H. (2018). Sampling with probability proportional to prediction: rethinking rapid plant diversity assessment. *Forestry: An International Journal of Forest Research*, 91, 17–26. <https://doi.org/10.1093/forestry/cpx044>
- Yoccoz, N.G., Nichols, J.D., & Boulinier, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution*, 16, 446–453. [https://doi.org/10.1016/S0169-5347\(01\)02205-4](https://doi.org/10.1016/S0169-5347(01)02205-4)

CHAPTER III

How mountain forests are changing: Resurvey of historical vegetation data in the Northern Apennines (Italy)

Chapter to be published as:

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ABSTRACT

Question: To what extent have the plant species assemblages of mountain forests changed during the past 60-80 years?

Location: Northern Apennines, Italy

Methods: In 2018, we resampled 22 historical vegetation plots recorded between 1934 and 1961 in three main forest types: i) European beech forests, ii) chestnut forests, and iii) oak forests. At present, these data are among the oldest vegetation plots available at European level for resurvey studies. Three replicates for each original plot were compared with the original data, in terms of forest structure, plant species richness and composition. To assess changes in species composition we ran PERMANOVA, NMDS ordination based on Bray-Curtis distance and beta diversity partitioning. Ellenberg indicator values were associated to each species to explore ecological changes in the assemblages.

Results: The final data set consisted of 88 plots (22 original and 66 resampled plots) and 366 plant species. All the sampled forests were originally managed, while currently almost all the sites are under abandonment. Species richness decreased in the herb and shrub layer, while increased in the tree layer. Species composition significantly differed between original and newly recorded plots, with changes mostly due to the replacement of light-demanding species with more shade-tolerant ones. Overall, forests are getting taller and darker. Chestnut and oak forests reached a more mixed composition as compared to the original plots, including several tree species typical of mixed-broadleaved forests.

Conclusions: Abandonment of mountain forests resulted in structural and compositional changes that would imply in a relatively short period the loss of cultural habitats, like chestnut orchards, as indicated by the increasing mixture in species composition of chestnut and oak forests, which are converging into mixed-broadleaved forests. However, these changes may be also the base for the recovery of natural dynamics and biodiversity in a broader spatio-temporal perspective.

Key-words: Beta diversity partitioning, Chestnut forests, European beech forests, Forest abandonment, Mountain forests, Oak forests, Pietro Zangheri, Species composition, Species richness.

<i>Contents</i>	<i>page</i>
1 Introduction	47
2 Materials and methods	48
2.1 Study area	48
2.2 Procedure of plot relocation	49
2.3 Data collection	50
2.4 Data analysis	50
3 Results	51
4 Discussion	55
Aknowledgements	57
Funding	57
References	57

1 Introduction

Dynamics of forest ecosystems have been largely driven by their millennia-long use (Bengtsson, Nilsson, Franc, & Menozzi, 2000). In the Apennine mountain chain, along the Italian peninsula, anthropogenic land use has had a profound effect on forests, in most cases outweighing by far the effects of macro-ecological constraints (Brown, Hatton, Selby, Leng, & Christie, 2013; Vacchiano, Garbarino, Lingua, & Motta, 2017).

Mountain forests have been used for timber, fuelwood, and cleared for agriculture or wooded pastures starting from the 8th century, under the Roman influence (Vacchiano et al., 2017). During the middle age, the European beech forests were the dominant forest type, with chestnut cultivation spreading at the lower and intermediate elevation belts, as a staple resource for fruit and timber production (Watson, 1996; Conedera, Krebs, Tinner, Pradella, & Torriani, 2004). Such intense use of mountain forests proceeded until the mid-twentieth century, even if fluctuations were experienced in relation to the periods of population decrease or increase, as well as with major historical events (Vacchiano et al., 2017). After the Second World War the mountain areas experienced a process of depopulation that continued till present days (Falcucci, Maiorano, & Boitani, 2007). The massive substitution of wood and charcoal by fossil fuels and changes in socio-economic processes determined a widespread abandonment of mountain settlements and a decrease in forest harvesting. This trend has boosted the ageing of most of the Apennine forests in the last decades, with subsequent structural and compositional changes (Vacchiano et al., 2017; Pezzi, Maresi, Conedera, & Ferrari, 2011; Burrascano et al., 2016).

The availability of historical vegetation data to compare with present-day species composition provides the potential to evaluate these changes. Thanks to a long tradition of collecting vegetation data according to the phytosociological approach (Braun-Blanquet, 1964), a huge amount of data (i.e., phytosociological relevés) at the plot scale (Chytrý, Tichý, Hennekens, & Schaminée, 2014) is currently available. Globally, millions of such plot data are stored in electronic databases, with a special focus on many European countries (Dengler et al., 2011; Jansen et al., 2012). These data represent an important source of information for monitoring habitat dynamics and resurvey studies are increasingly used for investigating long-term changes in plant species diversity and composition (Kapfer et al., 2017).

With this study, we aimed to investigate vegetation changes over the last 60-80 yrs in the mountain forests of the Northern Apennines, by resurveying vegetation data originally recorded between 1934 and 1961 (Zangheri, 1966). Original samples covered three main forest types: European beech forests, chestnut forests and oak forests. These data are much older than the majority of the

vegetation data available for resurvey studies (Jansen et al., 2012), thus providing the potential of investigating changes over long time slices.

We expect that (1) almost all the surveyed plots originally managed are nowadays under abandonment due to the trends mentioned above and we hypothesize that abandonment of management would promote: (2) structural changes in terms of increasing canopy coverage and tree height with the ageing of most of the Apennine forests, (3) shade tolerant herb species at the expense of species of open habitats (Becker, Spanka, Schröder, & Leuschner, 2017), (4) a convergence in the species composition of the different forest types due to lack of management and selection, especially on the tree layer (Pezzi et al., 2011).

2 Materials and methods

2.1 Study area

Pietro Zangheri was an experienced botanist (Zangheri, 1976) and a locally very famous naturalist, who produced several ecological and phytogeographical data (<http://www.pietrozangheri.it/>, Viciani, Gonnelli, Sirotti, & Agostini, 2010). We resurveyed 23 historical vegetation plots originally sampled by Zangheri (1966) between 1934 and 1961 in the mountain forests of the northern Apennines (*Figure 1*). Plots were located between the regions of Emilia-Romagna and Tuscany. Original surveys included three main forest types: European beech forests (14 plots), chestnuts forests (5 plots) and oak forests (4 plots). Fourteen sites are currently included in the Foreste Casentinesi National Park (FCNP), with ten of them being included in the Biogenetic Natural Reserves (RRNNBB) and three plots in the Sasso Fratino Integral Reserve (Bottacci, 2009). Elevations of the sites sampled by Zangheri (1966) range from 500 m to 1550 m, under mild climate conditions: an annual average temperature of 10°C (from 7°C at the highest elevations to 13°C at the lowest elevations) and a mean annual rainfall of 1335 mm (from 908 mm to 1612 mm, from the lowest to the highest sites). Climatic data refer to the period 1991-2015 for Emilia-Romagna and 1995-2014 for Tuscany. The prevalent bedrock consists of sandstones, arenaceous marls unit (Middle-lower Miocene) while soils are mainly dystric cambisol and calcareous cambisol (Geoportale Nazionale).

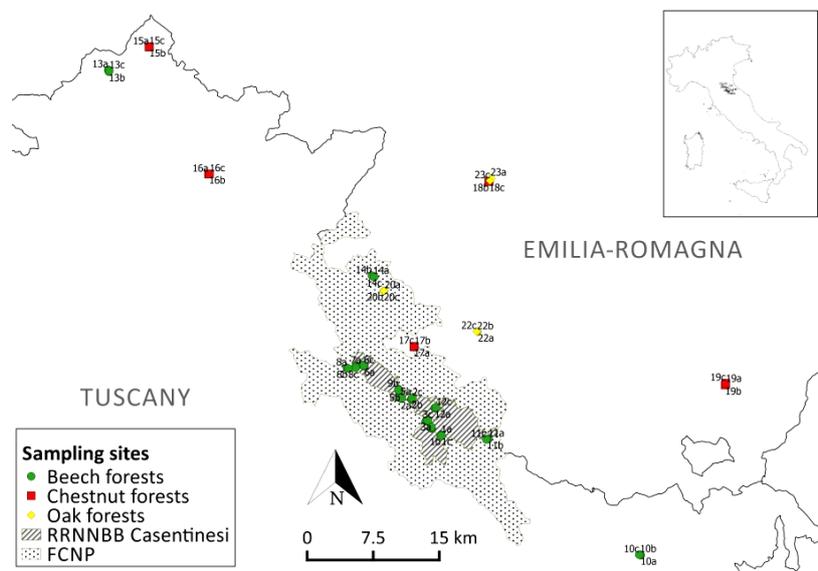


Figure 1 Location of the resurveyed forest vegetation plots. Sites are placed along the Northern Apennines, between the two administrative regions of Emilia-Romagna and Tuscany.

2.2 Procedure of plot relocation

Since the original vegetation plots did not have an exact geographic reference (i.e., they are quasi-permanent plots according to Kapfer et al., 2017), we first used locality name to identify a site for each original plot. Then, by means of a Digital Terrain Model with a fine grid of 20 m, we applied a stratified approach using the topographic information (i.e., elevation, slope and aspect) of each original plot to identify the points where the new sampling should be performed (Giarrizzo, Burrascano, & Zavattero, 2015; Giarrizzo et al., 2017).

Comparable vegetation coverage and the species composition of the original plots were also considered in the relocation process (Ross, Woodin, Hester, Thompson, & Birks, 2010; Kopecký and Macek, 2015; Britton, Hester, Hewison, Potts, & Ross, 2017). To compare vegetation coverage we used recent satellite imagery (Imagery ©2018 NASA, TerraMetrics; “openlayer” plugin, QGIS Development Team, 2016) and historical aerial photographs (available in the website of the Tuscan region), according to the sampling dates of the original plots. We used available historical aerial photographs also for checking the presence of roads or paths in the years of the historical surveys. For the original forest canopy structure and composition we did a direct comparison in the field looking at sites with occurrence of, at least, the dominant species of the original plots.

We sampled three replicates as close to the best estimate of the original plots as possible (Ross et al., 2010; Chytrý et al., 2014; Giarrizzo et al., 2017; Kapfer et al., 2017). As thresholds, we located replicates at a minimum distance of 50 m and a maximum of 200 m each other.

2.3 Data collection

We carried out the field work from May to July 2018. We recorded the species composition following a protocol aligned with the original surveyor and in the same period of the year (Chytrý et al., 2014; Becker et al., 2017; Giarrizzo et al., 2017). A complete list of plant species, differentiated by vegetation layers, and the percentage of coverage for each species were recorded. Layers were defined according to thresholds of height: herb layer ($H < 0.5$ m), shrub layer ($0.5 < H < 3.5$ m), tree layer ($H > 3.5$ m). Prevalent height and percentage of coverage were recorded for each layer. We sampled squared plots placed in the direction of the maximum slope, with plot size set to the same grain indicated in the original data (Britton et al., 2017; Förster, Becker, Gerlach, Meesenburg, & Leuschner, 2017), ranging from 40 to 100 square meters.

Special attention was paid to taxonomic standardization between the historical and newly recorded data sets. As reference for the nomenclature we followed Bartolucci et al. (2018) and all synonyms were recognized as a single species.

2.4 Data analysis

We analyzed structural differences between original and newly recorded plots by comparing the average height of the tree layer, the percentage of coverage of each layer (i.e., trees, shrubs, herbs), and the fraction of woody species in the herb layer.

We compared species richness (total species richness and species richness of each layer) for the whole data sets (original plots *vs.* resurvey) and separately for each forest type. We tested for significant differences using the Mann-Whitney-Wilcoxon Test (R function “*wilcox.test*”).

We tested differences in species composition between original and newly recorded plots with a PERMANOVA test (Anderson, 2001) based on 9999 permutations (function “*adonis*”, *vegan* R package, Oksanen et al., 2016). Then, to visualize changes in species assemblages we applied a non-metric multidimensional scaling (NMDS) with function “*metaMDS*” (*vegan* R package) based on Bray-Curtis distance.

In order to investigate if the variation in species composition of assemblages was mainly due to species replacement (i.e., turnover) or species loss (i.e., nestedness), we performed a beta diversity partitioning among turnover and nestedness (Baselga, 2010, 2012), with function “*beta-multi*” (*betapart* R package, Baselga, Orme, Villeger, De Bortoli, & Leprieur, 2018), using the Jaccard dissimilarity index on presence/absence data (Chytrý et al., 2014). We calculated pairwise beta diversity comparing each original plot with each of the three replicates and then we averaged the values of the indices (i.e., total beta diversity, nestedness and turnover) for the whole data sets (i.e., original *vs.* replicates) and separately for each forest type.

To investigate the ecological variation from the original to the newly recorded plots, we calculated unweighted mean Ellenberg indicator values (Pignatti, Menegoni, & Pietrosanti, 2005) evidencing the most relevant patterns (e.g., Becker et al., 2017).

All analyses were performed with the R statistical software version 3.4.2 (R Core Team, 2017).

3 Results

The final data set was composed of 88 plots (22 original and 66 new) and 366 plant species. Among the 23 original plots that were available, we did not relocate one plot due to lack of consistency with the current conditions of the area indicated in the original survey.

All the original plots were managed, while currently almost all the sites are abandoned, with the exception of two European beech forests (both in conversion to high forests) and two chestnut forests (one managed as coppice and one as orchard).

Species richness decreased (*Table 1*) both in the herb and shrub layer, while increased in the tree layer. At forest type level, European beech forests showed a decrease in the average species richness, with a significant reduction of species richness in the herb and shrub layers. Even for the chestnut and oak forests we found a decrease in the average species richness per plot, with a significant increase of species richness only in the tree layer (*Table 1*).

Table 1 – Species richness comparisons at data set and plot level (mean \pm SD). O = Original plots, R = Resurveyed plots, Beech = Beech forests, Chestnut = Chestnut forests, Oak = Oak forests. Grey background indicates significant differences between original and resurveyed plots (p-values $<$ 0.05, Mann-Whitney-Wilcoxon Test).

		SR tot	Herb layer	Shrub layer	Tree layer
Data sets	O	284	235	40	11
	R	239	227	36	25
Plots	O	38.8 \pm 10.9	30.9 \pm 9.3	6.1 \pm 4.4	1.7 \pm 0.9
	R	22.7 \pm 12.8	18.8 \pm 11.7	2.6 \pm 3.1	2.4 \pm 1.4
Beech	O	35.4 \pm 6.0	29.6 \pm 5.6	4.0 \pm 1.8	1.8 \pm 1.0
	R	17.1 \pm 7.1	6.6 \pm 4.6	1.2 \pm 2.0	1.9 \pm 0.9
Chestnut	O	47.8 \pm 10.9	38.8 \pm 11.2	7.6 \pm 2.6	1.0 \pm 0.0
	R	35.3 \pm 16.7	29.5 \pm 17.2	4.6 \pm 3.7	2.7 \pm 2.0
Oak	O	39.3 \pm 21.9	24.0 \pm 14.8	13.6 \pm 6.8	2.0 \pm 1.0
	R	27.7 \pm 9.5	20.5 \pm 8.0	5.5 \pm 2.4	4.0 \pm 0.9

The PERMANOVA test showed significant differences in species composition between the two sampling periods, both across the whole data set ($F = 4.873$, $R^2 = 0.054$, $P = 0.001$) and within all the individual groups (i.e., forest types) (European beech forests: $F = 5.320$, $R^2 = 0.090$, $P = 0.001$; Chestnut forests: $F = 3.679$, $R^2 = 0.170$, $P = 0.001$; Oak forests: $F = 2.682$, $R^2 = 0.211$, $P = 0.008$).

NMDS ordination showed a general shift between the species composition of the original and the newly recorded plots (*Figure 2*). This shift was mainly due to an increase in the canopy closure and height of the tree layer, consistent with an increase in shade-tolerant species (as shown by the

direction of the vector representing the ecological indicator value for light, *Figure 2*). Accordingly, among the other ecological indicator values, we evidenced an increasing soil acidification (with the decrease of R indicator value), likely due to the increase in tree biomass and leaf litter in the newly recorded stands. The other ecological indicator values (N, T, and U) resulted orthogonal to this shift in species composition (*Figure 2*), mostly reflecting vegetation gradients linked to elevation and other environmental variables.

The main differences were recorded for the tree layer composition of chestnut and oak forests, while beech forests were almost comparable between the two surveys. Chestnut (*Castanea sativa* Mill.) was the only tree species which characterized the original chestnut forests, while in the resurvey we found species typical of mixed-broadleaved forests: *Fagus sylvatica* L., *Acer pseudoplatanus* L., *Acer campestre* L., *Acer opalus* Mill., *Fraxinus ornus* L., and *Ostrya carpinifolia* Scop.. Oak forests were characterized by the dominance of two species in the tree layer of the original plots, i.e., *Quercus cerris* L. and *Quercus pubescens* Willd., while in the resurvey we found also *Acer opalus* Mill., *Fraxinus ornus* L., and, in all the newly recorded plots, *Ostrya carpinifolia* Scop.

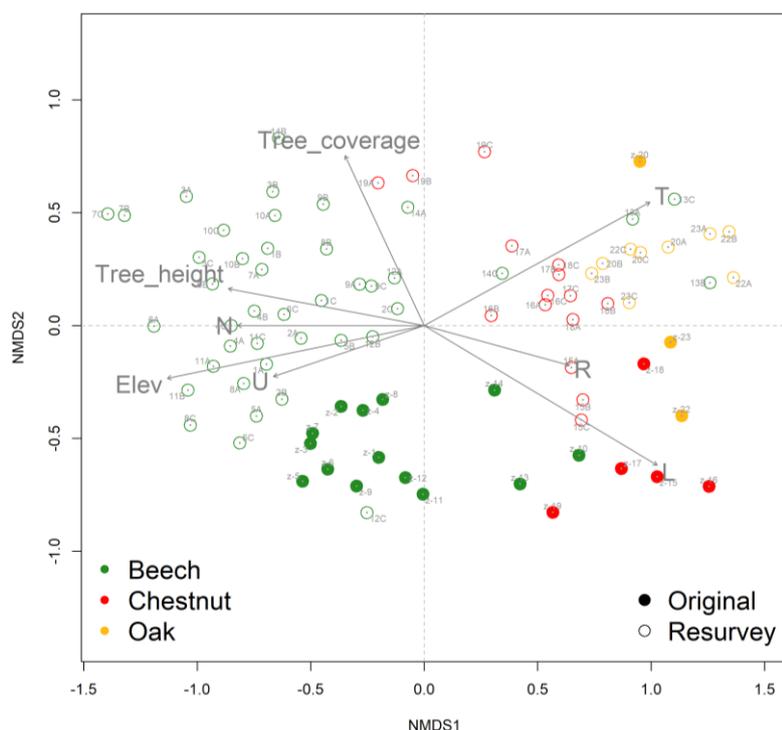


Figure 2 NMDS ordination performed for the whole data set. Plots are grouped for forest type (Beech forests = green; Chestnuts forests = red; Oak forests = yellow). Original and newly recorded (“Resurvey”) plots are shown with different symbols. Arrows: Ecological indicator values (L = Light; N = soil nutrients; R = soil pH; T = temperature; U = soil moisture), elevation (Elev), and structural attributes (Tree_height = average height of tree layer, Tree_coverage = canopy closure).

Variation in species composition for the whole data set and for each forest type (beta diversity) was mainly due to turnover (i.e., species replacement), with a low contribution of nestedness (i.e., species loss; *Figure 3*).

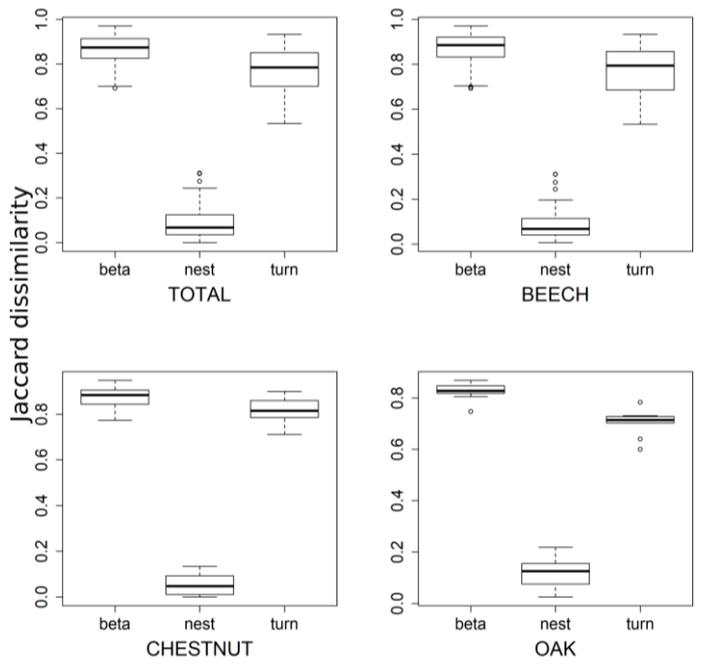


Figure 3 Beta diversity partitioning: total beta diversity (beta), nestedness (nest) and turnover (turn). Averaged pairwise comparisons for the whole data set and for each forest type separately (BEECH = beech forests, CHESTNUT = chestnut forests, OAK = oak forests).

Light-demanding species were replaced by more shade-tolerant ones. Indeed, species assemblages showed a significantly lower ecological indicator value for light in the replicate survey than in the original one, for the whole data set and even for each forest type (*Figure 4*).

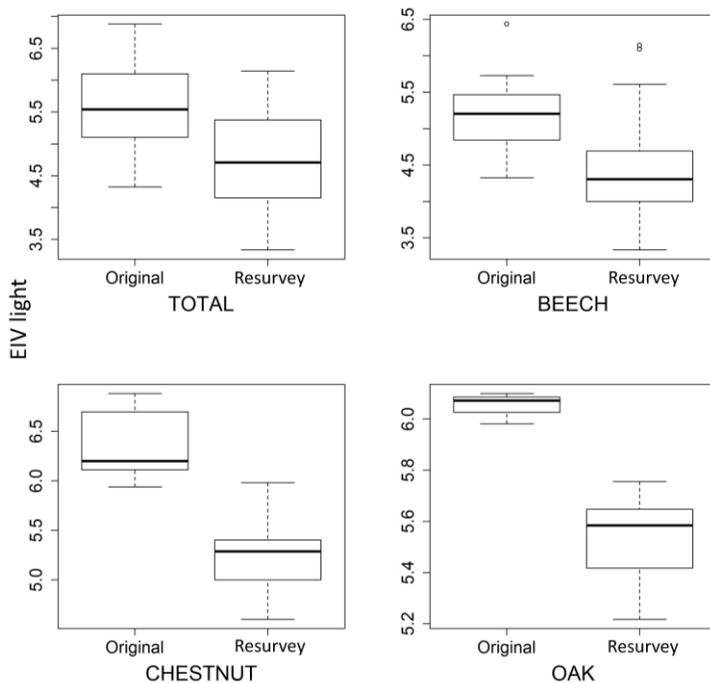


Figure 4 Comparison between the average ecological indicator values for light of the original and newly recorded plots, for the whole data set (TOTAL) and for each forest type separately (BEECH = beech forests, CHESTNUT = chestnut forests, OAK = oak forests). The Mann-Whitney-Wilcoxon test indicated significant differences between original and resurveyed plots in all the four cases (p-value < 0.05).

We found a significant increase of tree height and tree coverage, while shrub coverage decreased (*Table 2*). Considering the forest types separately, tree height increased significantly in oak forests, tree coverage in beech forests, while shrub coverage decreased in beech and oak forests. Finally, the

proportion of woody species in the herb layer increased from the original to the replicate survey in the three forest types (Table 2, Table 3).

Table 2 Structural comparison between original and newly recorded plots calculated for the whole data set and for each forest type. A = tree layer; B = shrub layer; C = herb layer; H mean = average height; coverage % = percentage of canopy coverage; woody species % = percentage of woody species in the herb layer. In bold: Significant differences between old and replicate plots (p-value < 0.05). The symbol * indicates significant differences (p-values < 0.05, Mann-Whitney-Wilcoxon Test) for the whole data set, irrespective of the forest type.

	Original	Resurvey	Original	Resurvey	Original	Resurvey
	Beech		Chestnut		Oak	
A - H mean*	17.7 ± 11.3	24.3 ± 7.7	9.9 ± 3.2	15.1 ± 4.9	6.3 ± 2.0	13.1 ± 3.5
A - coverage %*	49.6 ± 31.4	81.6 ± 16.8	56.0 ± 8.9	59.3 ± 28.5	45.3 ± 40.4	66.1 ± 18.2
B - coverage %*	25.1 ± 17.9	9.0 ± 20.4	29.0 ± 13.8	51.0 ± 34.9	66.6 ± 23.1	23.1 ± 18.2
C - coverage %	63.3 ± 30.2	41.7 ± 34.5	72.0 ± 17.8	68.2 ± 31.7	86.6 ± 23.1	82.7 ± 10.6
Woody species %*	1.3 ± 2.1	14.8 ± 10.8	1.8 ± 1.8	19.4 ± 8.4	1.0 ± 1.7	25.4 ± 12.5

Woody species recorded in the herb layer of the original plots did not correspond to the most frequent woody species in the resurvey and these latter largely included seedlings of several tree species almost absent from the herb layer in the original survey (Table 3).

Table 3 Woody species recorded in the herb layer. Only the first 10 species are reported, according to their relative occurrence within the plots of the same forest type (14 original plots in beech forests vs. 42 resurveys; 5 original plots in chestnut forests vs. 15 resurveys; 3 original plots in oak forests vs. 9 resurveys). Freq = relative occurrence.

	ORIGINAL		RESURVEY	
BEECH FORESTS	Species (3 out of 3)	Freq	Species (10 out of 26)	Freq
	<i>Rubus caesius</i>	0.21	<i>Acer pseudoplatanus</i>	0.40
	<i>Lonicera caprifolium</i>	0.07	<i>Abies alba</i>	0.26
	<i>Rubus ulmifolius</i>	0.07	<i>Rubus hirtus</i>	0.21
	-	-	<i>Laburnum alpinum</i>	0.19
	-	-	<i>Fagus sylvatica subsp. sylvatica</i>	0.12
	-	-	<i>Fraxinus excelsior subsp. excelsior</i>	0.12
	-	-	<i>Sorbus aucuparia subsp. aucuparia</i>	0.12
	-	-	<i>Sambucus nigra</i>	0.10
	-	-	<i>Corylus avellana</i>	0.07
-	-	<i>Quercus cerris</i>	0.07	
CHESTNUT FORESTS	Species (2 out of 2)	Freq	Species (10 out of 27)	Freq
	<i>Rubus ulmifolius</i>	0.60	<i>Rubus hirtus</i>	0.47
	<i>Polygala chamaebuxus</i>	0.20	<i>Acer opalus</i>	0.40
	-	-	<i>Crataegus monogyna</i>	0.40
	-	-	<i>Laburnum anagyroides subsp. anagyroides</i>	0.33
	-	-	<i>Rosa canina</i>	0.33
	-	-	<i>Acer campestre</i>	0.27
	-	-	<i>Castanea sativa</i>	0.27
	-	-	<i>Fraxinus ornus</i>	0.27
	-	-	<i>Acer pseudoplatanus</i>	0.20
-	-	<i>Cornus sanguinea</i>	0.20	
OAK FORESTS	Species (2 out of 2)	Freq	Species (10 out of 27)	Freq
	<i>Lonicera caprifolium</i>	0.33	<i>Fraxinus ornus</i>	0.78
	<i>Polygala chamaebuxus</i>	0.33	<i>Acer opalus</i>	0.56
	-	-	<i>Emerus major subsp. major</i>	0.44
	-	-	<i>Cornus mas</i>	0.33
	-	-	<i>Lonicera xylosteum</i>	0.33
	-	-	<i>Acer campestre</i>	0.22
	-	-	<i>Cornus sanguinea</i>	0.22
	-	-	<i>Crataegus monogyna</i>	0.22
	-	-	<i>Quercus pubescens subsp. pubescens</i>	0.22
-	-	<i>Rosa canina</i>	0.22	

4 Discussion

The resurvey of historical vegetation plots along the Northern Apennine ridge highlighted the consequences in the structure, as well as in species diversity and composition, of plant communities resulting from the abandonment of mountain forests (Vacchiano et al., 2017). Indeed, as compared to the original survey from 1934-1961 up to the present, forests are getting taller and darker, with a general replacement of light-demanding species with more shade-tolerant species and with herb and shrub layers currently poorer in species. Especially species assemblages of chestnut and oak forests are showing an increasing mixture, with a trend toward mixed-broadleaved forests. The great increase in the frequency of tree regeneration in the herb layer is an additional clue of a long term dynamic process.

The reduction of species richness in the herb and shrub layer may be due to habitat specialization and loss of micro-habitat heterogeneity imposed by the closure of forest canopies, consistent with a decrease in the richness of light-demanding or open-habitat species (e.g., Amici et al., 2013). Indeed, species richness of vascular plants has been advocated as indicator of disturbance more than of conservation status for forest ecosystems (Boch et al., 2013), since plants may benefit from resource increase (such as light or nutrients) related to moderate disturbance by management or other human uses (Roberts, 2004; Christensen & Heilmann-Clausen, 2009; Nascimbene, Fontana, & Spitale, 2014). Further, canopy closure may be likely linked also to an increasing tree biomass and soil acidification, as indicated by the decrease of R indicator value from the original to the newly recorded plots (Persson, Malmer, & Wallén, 1987).

Abandonment of forest patches may be planned as part of a rewilding strategy aimed at promoting the recovery of natural processes, functions and biodiversity (e.g., Chiarucci & Piovesan, 2018; Sitzia, Campagnaro, Gatti, Sommacal, & Kotze, 2015; Watson et al., 2018), set-asides being one of the key elements of integrative approaches for conservation (Vandekerkhove, Thomaes, & Jonsson, 2013). Notwithstanding, forest abandonment may imply also the loss of cultural forests that were part of a traditional agro-silvicultural land-use system and were shaped by centuries – or even millennia – of human use (Bollmann & Braunisch, 2013; Mölder, Streit, & Schmidt, 2015). This is the case of chestnut forests (orchards and coppices), which are considered among the most typical elements of the southern European mountain landscape (Pezzi et al., 2011) and in the European Union are habitat of conservation concern according to the “*Habitat*” directive (Directive 92/43/EEC). Abandonment of management activities would imply a gradual loss of this habitat, with the establishment of several broadleaved species and consequent changes in structure and species assemblages (Pezzi et al., 2011) converging into mixed-broadleaved stands. However, it should be also considered that our findings refer to a small spatial scale and even to a limited temporal scale as compared to the time and space necessary for the development of natural

processes, functions and diversity in the forest ecosystems (e.g., Nascimbene, Dainese, & Sitzia, 2013; Kaufmann, Hauck, & Leuschner, 2017; Schall et al., 2018; Watson et al., 2018).

At present, the conservation of multiple facets of forest diversity should be planned at landscape level, considering the contribution of traditional forest practices to structural and compositional diversity (Bollmann & Braunisch, 2013), but ensuring also the protection, and institution, of set-asides for allowing the recovery of natural dynamics and biodiversity over long time.

The availability of historical vegetation data represents an important source of information for detecting changes over time and for orienting conservation. However, it should be carefully taken into account that the accuracy of comparative studies between original and newly recorded plots may be biased due to observer and relocation errors (Verheyen et al., 2018), with consequent risk of pseudo-turnover adding a random error to the temporal change in vegetation (Kapfer et al., 2017), e.g., recorded changes in species composition may be caused by sampling a different place, and not by actual species turnover. Observer and relocation errors are non-negligible when resurveying quasi-permanent plots and Verheyen et al. (2018) warns about interpretation of the results of resurvey studies especially when changes in richness are assessed based on a low number of plots. Notwithstanding, some measures may maximally increase the precision of the inferences, such as the resurvey of more than one plot for each original plot (i.e., replicates) as close to the best estimate of the original plot as possible and the standardization of the resurvey, aligning the protocol with that followed by the original surveyor (Becker et al., 2017). Accordingly, to reduce relocation errors, we (1) replicated three plots for each original sample, avoiding direct comparisons plot-to-plot, (2) adopted the same sampling size (Hédl, 2004; Förster et al., 2017; Britton et al., 2017), (3) repeated the samples in the same season of the original survey, to minimize errors due to phenological differences (Chytrý et al., 2014), and (4) considered species composition of the original survey, especially the dominant species, when relocating the samples in the field (Ross et al., 2010; Kopecký & Macek, 2015; Kapfer et al. 2016; Britton et al., 2017; Vild et al., 2017). Furthermore, the availability of historical vegetation maps (Giarrizzo et al., 2015), or historical aerial photographs, of the same period of the original survey, may greatly help the relocation of plots according to the vegetation patterns and the original accessibility of the potential sampling sites. Concluding, in this study we recorded changes in mountain forest vegetation of the Northern Apennines which are consistent with the well-known processes of abandonment of mountain settlements due to changes in socio-economic dynamics in the second half of the 20th century. This trend is part of a general process of land-use polarization that is being observed across Europe (Jepsen et al., 2015) with some forests, especially plantations, that are being managed more intensively than in the past, while other forests mostly located in less-accessible places, are currently managed less intensively than in the past, or even abandoned, as in our study case

(Burrascano et al., 2016). Besides the recognized primary role of cultural/anthropogenic processes (i.e., management-driven processes) as drivers of forest diversity, structure and composition, climate change scenarios with all the cascade effects on biodiversity (e.g., Christenson, Mitchell, Groffman, & Lovett, 2014; Harris et al., 2018; Guo, Lenoir, & Bonebrake, 2018) urgently claims for additional studies to disentangle the effects of land-use and climate, but also to investigate their interactions as drivers of changes. These studies represent an important basis for planning scientifically sounds adaptive interventions and conservation strategies.

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References

- Amici, V., Santi, E., Filibeck, G., Diekmann, M., Geri, F., Landi, S., ... Chiarucci, A. (2013). Influence of secondary forest succession on plant diversity patterns in a Mediterranean landscape. *Journal of Biogeography*, *40*, 2335–2347. <https://doi.org/10.1111/jbi.12182>
- Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, *26*, 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Bartolucci, F., Peruzzi, L., Galasso, G., Albano, A., Alessandrini, A., Ardenghi, ... Conti, F. (2018). An updated checklist of the vascular flora native to Italy. *Plant Biosystems*, *152*, 179–303. <https://doi.org/10.1080/11263504.2017.1419996>
- Baselga, A. (2010). Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, *19*, 134–143. <https://doi.org/10.1111/j.1466-8238.2009.00490.x>
- Baselga, A. (2012). The relationship between species replacement, dissimilarity derived from nestedness, and nestedness. *Global Ecology and Biogeography*, *21*, 1223–1232. <https://doi.org/10.1111/j.1466-8238.2011.00756.x>
- Baselga A., Orme D., Vileger S., De Bortoli J., & Leprieur F. (2018, October 17). betapart: Partitioning Beta Diversity into Turnover and Nestedness Components. R package version 1.4-1. Retrieved from <https://CRAN.R-project.org/package=betapart>
- Becker, T., Spanka, J., Schröder, L., & Leuschner, C. (2017). Forty years of vegetation change in former coppice-withstandards woodlands as a result of management change and N deposition. *Applied Vegetation Science*, *20*, 304–313. <https://doi.org/10.1111/avsc.12282>
- Bengtsson, J., Nilsson, S.G., Franc, A., & Menozzi, P. (2000). Biodiversity, disturbances, ecosystem function and management of european forests. *Forest Ecology and Management*, *132*, 39–50. [https://doi.org/10.1016/S0378-1127\(00\)00378-9](https://doi.org/10.1016/S0378-1127(00)00378-9)
- Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., ... Fischer, M. (2013). High plant species richness indicates management-related disturbances rather than the conservation status of forests. *Basic and Applied Ecology*, *14*, 496–505. <https://doi.org/10.1016/j.baae.2013.06.001>
- Bollmann K., & Braunisch V. (2013). To integrate or to segregate: balancing commodity production and biodiversity

- conservation in European forests. In: Kraus, D., & Krumm, F. (Eds.). *Integrative approaches as an opportunity for the conservation of forest biodiversity* (pp. 18-31). European Forest Institute.
- Bottacci A. (Ed.) (2009). *La Riserva Naturale Integrata di Sasso Fratino: 1959-2009. 50 anni di conservazione della biodiversità*. CFS/UTB Pratovecchio, Italy.
- Braun-Blanquet J. (1964). *Pflanzensoziologie. Grundzüge der Vegetationskunde* (3rd ed.). Springer, Berlin.
- Britton, A.J., Hester, A.J., Hewison, R.L., Potts, J.M., & Ross, L.C. (2017). Climate, pollution and grazing drive long-term change in moorland habitats. *Applied Vegetation Science*, 20, 194–203. <https://doi.org/10.1111/avsc.12260>.
- Brown, A.G., Hatton, J., Selby, K.A., Leng, M.J., & Christie, N. (2013). Multi-proxy study of Holocene environmental change and human activity in the Central Apennine Mountains, Italy. *Journal of Quaternary Science*, 28, 71–82. <https://doi.org/10.1002/jqs.2591>
- Burrascano, S., Chytrý, M., Kuemmerle, T., Giarrizzo, E., Luysaert, S., Sabatini, F.M., & Blasi, C. (2016). Current European policies are unlikely to jointly foster carbon sequestration and protect biodiversity. *Biological Conservation*, 201, 370–376. <https://doi.org/10.1016/j.biocon.2016.08.005>
- Chiarucci, A., & Piovesan, G. (2018). Sustainable forest management can not disregard the current knowledge on ecology and conservation. *Forest@ - Rivista di Selvicoltura ed Ecologia Forestale*, 15, 51–55. doi: 10.3832/efor2782-015
- Christensen, M., & Heilmann-Clausen, J. (2009). Forest biodiversity gradients and the human impact in Annapurna Conservation Area, Nepal. *Biodiversity and Conservation*, 18, 2205–2221. <https://doi.org/10.1007/s10531-009-9583-9>
- Christenson, L.M., Mitchell, M.J., Groffman, P.M., & Lovett, G.M. (2014). Cascading Effects of Climate Change on Forest Ecosystems: Biogeochemical Links Between Trees and Moose in the Northeast USA. *Ecosystems*, 17, 442–457. <https://doi.org/10.1007/s10021-013-9733-5>
- Chytrý, M., Tichý, L., Hennekens, S.M., & Schaminée, J.H.J. (2014). Assessing vegetation change using vegetation-plot databases: A risky business. *Applied Vegetation Science*, 17, 32–41. <https://doi.org/10.1111/avsc.12050>
- Conedera, M., Krebs, P., Tinner, W., Pradella, M., & Torriani, D. (2004). The cultivation of *Castanea sativa* (Mill.) in Europe, from its origin to its diffusion on a continental scale. *Vegetation History and Archaeobotany*, 13, 161–179. <https://doi.org/10.1007/s00334-004-0038-7>
- Dengler, J., Jansen, F., Glöckler, F., Peet, R.K., de Cáceres, M., Chytrý, M., ... Spencer, N. (2011). The Global Index of Vegetation-Plot Databases (GIVD): A new resource for vegetation science. *Journal of Vegetation Science*, 22, 582–597. <https://doi.org/10.1111/j.1654-1103.2011.01265.x>
- Falcucci, A., Maiorano, L., & Boitani, L. (2007). Changes in land-use/land-cover patterns in Italy and their implications for biodiversity conservation. *Landscape Ecology*, 22, 617–631. <https://doi.org/10.1007/s10980-006-9056-4>
- Förster, A., Becker, T., Gerlach, A., Meesenburg, H., & Leuschner, C. (2017). Long-term change in understorey plant communities of conventionally managed temperate deciduous forests: effects of nitrogen deposition and forest management. *Journal of Vegetation Science*, 28, 747–761. <https://doi.org/10.1111/jvs.12537>
- Geoportale Nazionale (2018, June 1). Carta geologica d'Italia alla scala 1:500.000 (2013). Retrieved from <http://www.pcn.minambiente.it>
- Giarrizzo, E., Burrascano, S., & Zattero, L. (2015). New methodological insights for the assessment of temporal changes in semi-natural dry grasslands plant species composition based on field data from the northern Apennines. *Hacquetia*, 14, 19–32. <https://doi.org/10.1515/hacq-2015-0014>
- Giarrizzo, E., Burrascano, S., Chiti, T., de Bello, F., Lepš, J., Zattero, L., & Blasi, C. (2017). Re-visiting historical semi-natural grasslands in the Apennines to assess patterns of changes in species composition and functional traits. *Applied Vegetation Science*, 20, 247–258. <https://doi.org/10.1111/avsc.12288>
- Guo, F., Lenoir, J., & Bonebrake, T.C. (2018). Land-use change interacts with climate to determine elevational species redistribution. *Nature Communications*, 9, 1–7. <https://doi.org/10.1038/s41467-018-03786-9>
- Harris, R.M.B., Beaumont, L.J., Vance, T.R., Tozer, C.R., Remenyi, T.A., Perkins-Kirkpatrick, S.E., ... Bowman, D.M.J.S. (2018). Biological responses to the press and pulse of climate trends and extreme events. *Nature Climate Change*, 8, 579–587. <https://www.nature.com/articles/s41558-018-0187-9>
- Hédl, R. (2004). Vegetation of beech forests in the Rychlebské Mountains, Czech Republic, re-inspected after 60 years with assessment of environmental changes. *Plant Ecology*, 170, 243–265. <https://doi.org/10.1023/B:VEGE.0000021681.83068.53>
- Jansen, F., Glöckler, F., Chytrý, M., De Cáceres, M., Ewald, J., Finckh, M., ... Dengler, J. (2012). News from the Global Index of Vegetation-Plot Databases (GIVD): the metadata platform, available data, and their properties. *Biodiversity & Ecology*, 4, 77–82. <https://doi.org/10.7809/b-e.00061>
- Jepsen, M.R., Kuemmerle, T., Müller, D., Erb, K., Verburg, P.H., Haberl, H., Vesterager, J.P., ... Reenberg, A. (2015). Transitions in European land-management regimes between 1800 and 2010. *Land use policy*, 49, 53–64. <https://doi.org/10.1016/j.landusepol.2015.07.003>
- Kapfer, J., Hédl, R., Jurasinski, G., Kopecký, M., Schei, F.H., & Grytnes, J.A. (2017). Resurveying historical vegetation data – opportunities and challenges. *Applied Vegetation Science*, 20, 164–171. <https://doi.org/10.1111/avsc.12269>
- Kaufmann, S., Hauck, M., & Leuschner, C. (2017). Comparing the plant diversity of paired beech primeval and

- production forests: Management reduces cryptogam, but not vascular plant species richness. *Forest Ecology and Management*, 400, 58–67. <https://doi.org/10.1016/j.foreco.2017.05.043>
- Kopecký, M., & Macek, M. (2015). Vegetation resurvey is robust to plot location uncertainty. *Diversity and Distributions*, 21, 322–330. <https://doi.org/10.1111/ddi.12299>
- Mölder, A., Streit, M., & Schmidt, W. (2014). When beech strikes back: How strict nature conservation reduces herb-layer diversity and productivity in Central European deciduous forests. *Forest Ecology and Management*, 319, 51–61. <https://doi.org/10.1016/j.foreco.2014.01.049>
- Müllerová, J., Hédl, R., & Szabó, P. (2015). Coppice abandonment and its implications for species diversity in forest vegetation. *Forest Ecology and Management*, 343, 88–100. <https://doi.org/10.1016/j.foreco.2015.02.003>
- Nascimbene, J., Dainese, M., & Sitzia, T. (2013). Contrasting responses of epiphytic and dead wood-dwelling lichen diversity to forest management abandonment in silver fir mature woodlands. *Forest Ecology and Management*, 289, 325–332. <https://doi.org/10.1016/j.foreco.2012.10.052>
- Nascimbene J., Fontana V., & Spitale D. (2014). A multi-taxon approach reveals the effect of management intensity on biodiversity in Alpine larch grasslands. *Science of the Total Environment*, 487, 110–116. <https://doi.org/10.1016/j.scitotenv.2014.04.013>
- Oksanen J., Blanchet F.G., Kindt R., Legendre P., Minchin P.R., O'Hara R.B., ... Wagner H. (2016). Vegan: ecological diversity. R package version 2.4–2. Retrieved from: <https://cran.r-project.org/web/packages/vegan/index.html> (accessed 8 January 2019)
- Persson, S., Malmer, N., & Wallén, B. (1987). Leaf litter fall and soil acidity during half a century of secondary succession in a temperate deciduous forest. *Plant Ecology*, 73, 31–45. <https://doi.org/10.1007/BF00031849>
- Pezzi, G., Maresi, G., Conedera, M., & Ferrari, C. (2011). Woody species composition of chestnut stands in the Northern Apennines: The result of 200 years of changes in land use. *Landscape Ecology*, 26, 1463–1476. <https://doi.org/10.1007/s10980-011-9661-8>
- Pignatti, S., Menegoni, P., & Pietrosanti, S. (2005). Biondificazione attraverso le piante vascolari. Valori di indicazione secondo Ellenberg (Zeigerwerte) per le specie della Flora d'Italia. *Braun-Blanquetia*, 39, 1–97.
- QGIS Development Team (2016). QGIS Geographic Information System. Open Source Geospatial Foundation Project. Retrieved from <http://qgis.osgeo.org>. (accessed 8 January 2019).
- R Core Team (2017). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from <https://www.R-project.org/> (accessed 8 January 2019).
- Roberts, M. R. (2004). Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany*, 82, 1273–1283. <https://doi.org/10.1139/b04-091>
- Ross, L.C., Woodin, S.J., Hester, A., Thompson, D.B.A., & Birks, H.J.B. (2010). How important is plot relocation accuracy when interpreting re-visitation studies of vegetation change? *Plant Ecology & Diversity*, 3, 1–8. <https://doi.org/10.1080/17550871003706233>
- Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., ... Ammer, C. (2018). The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *Journal of Applied Ecology*, 55, 267–278. <https://doi.org/10.1111/1365-2664.12950>
- Sitzia, T., Campagnaro, T., Gatti, E., Sommacal, M., & Kotze, D.J. (2015). Wildlife conservation through forestry abandonment: Responses of beetle communities to habitat change in the Eastern Alps. *European Journal of Forest Research*, 134, 511–524. <https://doi.org/10.1007/s10342-015-0868-0>
- Vacchiano, G., Garbarino, M., Lingua, E., & Motta, R. (2017). Forest dynamics and disturbance regimes in the Italian Apennines. *Forest Ecology and Management*, 388, 57–66. <https://doi.org/10.1016/j.foreco.2016.10.033>
- Vandekerkhove K., Thomaes A., & Jonsson B.-G. (2013). Connectivity and fragmentation: island biogeography and metapopulation applied to old-growth elements. In: Kraus, D., Krumm, F. (Eds.). *Integrative approaches as an opportunity for the conservation of forest biodiversity* (pp. 104–115). European Forest Institute.
- Verheyen, K., Bažány, M., Čečko, E., Chudomelová, M., Closset-Kopp, D., Czortek, P., ... Baeten, L. (2018). Observer and relocation errors matter in resurveys of historical vegetation plots. *Journal of Vegetation Science*, 29, 812–823. <https://doi.org/10.1111/jvs.12673>
- Vild, O., Hédl, R., Kopecký, M., Szabó, P., Suchánková, S., & Zouhar, V. (2017). The paradox of long-term ungulate impact: increase of plant species richness in a temperate forest. *Applied Vegetation Science*, 20, 282–292. <https://doi.org/10.1111/avsc.12289>
- Viciani, D., Gonnelli, V., Sirotti, M., & Agostini, N. (2010). An annotated check-list of the vascular flora of the “Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna” (Northern Apennines Central Italy). *Webbia*, 65, 3–131. <https://doi.org/10.1080/00837792.2010.10670867>
- Watson, C.S. (1996). The vegetational history of the northern Apennines, Italy: information from three new sequences and a review of regional vegetational change. *Journal of Biogeography*, 23, 805–841. <https://doi.org/10.1111/j.1365-2699.1996.tb00041.x>
- Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., ... Lindenmayer, D. (2018). The exceptional value of intact forest ecosystems. *Nature Ecology & Evolution*, 2, 599–610. <https://doi.org/10.1038/s41559-018-0490-x>
- Zangheri, P. (1966). Flora e vegetazione del medio ed alto appennino romagnolo. *Webbia*, 21, 1–450. <https://doi.org/10.1080/00837792.1966.10669838>
- Zangheri, P. (1976). *Flora italica*. CEDAM, Padova.

CHAPTER IV

Response of vascular plants and epiphytes to management and abandonment in mountain beech forests of the Northern Apennines (Italy)

Chapter to be published as:

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ABSTRACT

Questions: (1) To what extent is abandonment vs. management of mountain beech forests reflected in the species richness and composition of epiphytes and vascular plants? (2) Does habitat structure, topography or climate have the main influence on species composition of epiphytes and vascular plants?

Location: Foreste Casentinesi National Park, Northern Apennines (Italy).

Methods: We selected 10 managed and 10 abandoned stands in comparable topographical and climatic conditions and with a common management history. Within each stand we sampled a maximum of three squared plots 20 m x 20 m with thresholds of distances, for a total of 55 plots. Species frequency of vascular plants and epiphytes was recorded within each plot. (1) For answering the first question, we tested for significant differences in species richness of the three taxa between managed and abandoned stands. With an indicator species analysis we analyzed the association of species with managed vs. abandoned stands and harvesting periods. (2) For the second question, we tested the effect of individual structural, topographical and climatic variables on the species composition of the three taxa, through PERMANOVA and NMDS ordination, and classifying the species for habitat and substratum affiliation in order to underline particular ecological patterns.

Results: We recorded 113 species of vascular plants, 60 species of lichens and 17 species of bryophytes. (1) The species richness per treatment (i.e., managed vs. abandoned stands) was similar both for vascular plants and epiphytes. Only the species composition of vascular plants significantly differed between the two treatments, with indicator species of managed stands generalist for habitat affiliation. (2) Narrow-range species (in terms of habitat and substratum affiliation) of vascular plants and lichens were related to changes in forest structure, while changes in topography and climate were mostly related to the occurrence of generalist species. Bryophytes were influenced by climate and topography, but all the few sampled species were highly generalist for habitat and substratum affiliation.

Conclusions: The abandonment of forest management practices dating back 60-70 years ago is still not sufficient to evidence clear differences in species-richness and composition of the epiphytes, while vascular plants showed an already evident response. Further, irrespective of management or abandonment, conservation actions should take into account that, more than topography and climate, suitable habitat structures are key for the occurrence of specialist species in the investigated mountain beech forests.

Key-words: Bryophytes, Climate, *Fagus sylvatica*, Foreste Casentinesi National Park, Human footprint, Lichens, PERMANOVA, Specialist species, Species richness, Species composition, Structure, Topography.

<i>Contents</i>	<i>page</i>
1 Introduction	62
2 Materials and methods	63
2.1 Study area	63
2.2 Sampling design	64
2.3 Species inventory	65
2.4 Structural and environmental features	65
2.5 Data analysis	66
3 Results	68
3.1 Managed vs. Abandoned stands	68
3.2 Effect of topography, climate and forest structure on species composition	71
4 Discussion	73
4.1 Management vs. Abandonment	73
4.2 Effects of structure, topography and climate in shaping species assemblages	74
4.3 Management implications	75
Aknowledgements	76
References	76

1 Introduction

Fagus sylvatica L. is the most abundant deciduous tree species of the European temperate zone, extending from the mountains of southern Europe to the lowlands of southern England and southern Sweden and realizing a very broad ecological niche (Leuschner et al., 2006; Willner et al., 2009).

For centuries European beech forests have been transformed by human management with far-reaching effects on forest structure and biodiversity (Brunet et al., 2010). In Europe, beech forests had been kept for pasture and pannage (feeding pigs with beech nuts) for many centuries and selectively cut for wood, until the introduction of regular forestry in the 18th and 19th centuries. Coppice management was also common for the production of firewood and charcoal. During the 19th century, with the replacement of fossil to wood as primary source of energy and with the increasing demand of timber for construction, shelterwood system began the dominant beech forest management in most European countries (Brunet et al., 2010). Shelterwood management results in large, single-layered and even-aged beech stands, with a rotation period of 90–140 yrs, depending on soil fertility. This management system involves the thinning of the canopy to establish a dense natural regeneration, and the cut of the remaining seed trees after successful regeneration.

Given this long history of management, old-growth European beech forests are currently rare and fragmented, covering less than 1% of Europe's forest area, despite their outstanding importance for protection of functions, processes and biodiversity (Sabatini et al., 2018). In Italy, European beech forests dominate the mountain belt (Willner et al., 2009). These forests have been largely managed as coppices until the '60s, exploiting the vegetative resprouting capacity of beech trees (Campetella et al., 2016). After the Second World War, with changing economic and societal demands, most of the mountain beech forests have been subjected to a process of (i) conversion into high stands, or (ii) abandonment (Vacchiano et al., 2017; Sitzia et al., 2010). The conversion process consists in a progressive thinning (approximately every 15 years) and final harvest (after 110-140 years ca), with a consequent regeneration by seeds. Most of the managed beech stands are still in this type of transition (Nocentini, 2009). Forest abandonment may give rise to a process of rewilding (Sitzia et al., 2015) with a slowly recover of those structural features (e.g., deadwood, large living trees, presence of canopy openings, layering) typical of the old-growth forests (Bauhus et al., 2009; Vandekerckhove et al., 2009; Burrascano et al., 2013; Paillet et al., 2015).

In Europe, there is a wealth of studies on the effects of beech forest management on biodiversity (e.g., Paillet et al., 2010; Boch et al., 2013; Schall et al., 2018). These studies evidenced the importance of a multi-taxon framework since taxa exploiting different resources show contrasting patterns and sensitivity to habitat changes. For instance, vascular plants resulted to benefit from resource increase (e.g., light and nutrients) following moderate disturbance by management

(Roberts, 2004) and have been suggested as indicator of disturbance rather than of conservation status of the forests (Boch et al., 2013). On the contrary, demanding species of other taxa such as epiphytes, saproxylic fungi or saproxylic beetles, decreased due to the lack of suitable habitat conditions (e.g., large senescent trees, deadwood) in most of the managed stands (Kraus and Krumm, 2013).

In Italy, the effects of forest abandonment vs. the conversion into high stands in the mountain beech forests have been investigated in previous studies which focused on the response of vascular plants to forest structure (Scolastri et al., 2016; Scolastri et al., 2017; Burrascano et al., 2017). With this study, we aimed to contribute to a better understanding of this issue, investigating also the response of epiphytes (i.e., lichens and bryophytes), in the mountain beech forests of the Northern Apennines. Further, we investigated the effects of topography and climate in addition to forest structure. In fact, especially on mountains even topography may play a major role in shaping forest communities, exacerbating also climatic differences with substantial changes that can be found over small distances (Janssen et al., 2018).

Specifically, in the Foreste Casentinesi National Park, characterized by high forest continuity and connectivity, we compared European beech forest stands managed with the coppice selection system until the '60s and then abandoned or converted into high forests. We aimed to answer the following questions: (1) To what extent is the ongoing abandonment process compared to management reflected in the species richness and composition of the dwellers species? (2) Does habitat structure, topography or climate have the main influence on species composition of epiphytes and vascular plants?

2 Materials and methods

2.1 Study area

The study area is located within the Foreste Casentinesi National Park (FCNP). This protected area extends over an area of about 368.43 km², stretching across the ridge of the northern Apennines from 400 to 1657 m a.s.l.. Almost 85% of its surface is covered by forests, of which the beech forests cover the 40% of the forest area and the 35% of the total Park surface, in a system characterized by high forest connectivity (*Figure 1*). We specifically focused on the beech forests located in the Casentino valley, Tuscany (43°50' N, 11°45' E). These forests have been described as part of the *Geranio nodosi-Fagion* (Viciani and Agostini, 2008). The annual average temperature of the sampled sites is 8.9°C, ranging from 8°C at the highest elevations and 10°C at the lowest elevations, with an average annual maximum of 11.5°C, and minimum of 6.2°C; mean annual rainfall is 1357 mm, ranging from 1300 mm to 1420 mm from North-West to South-East

(Consorzio Lamma, data 1995-2014). The most common forest soils are cambisols with the bedrock consisting of sanstones, arenaceous marls (Geoportale Nazionale).

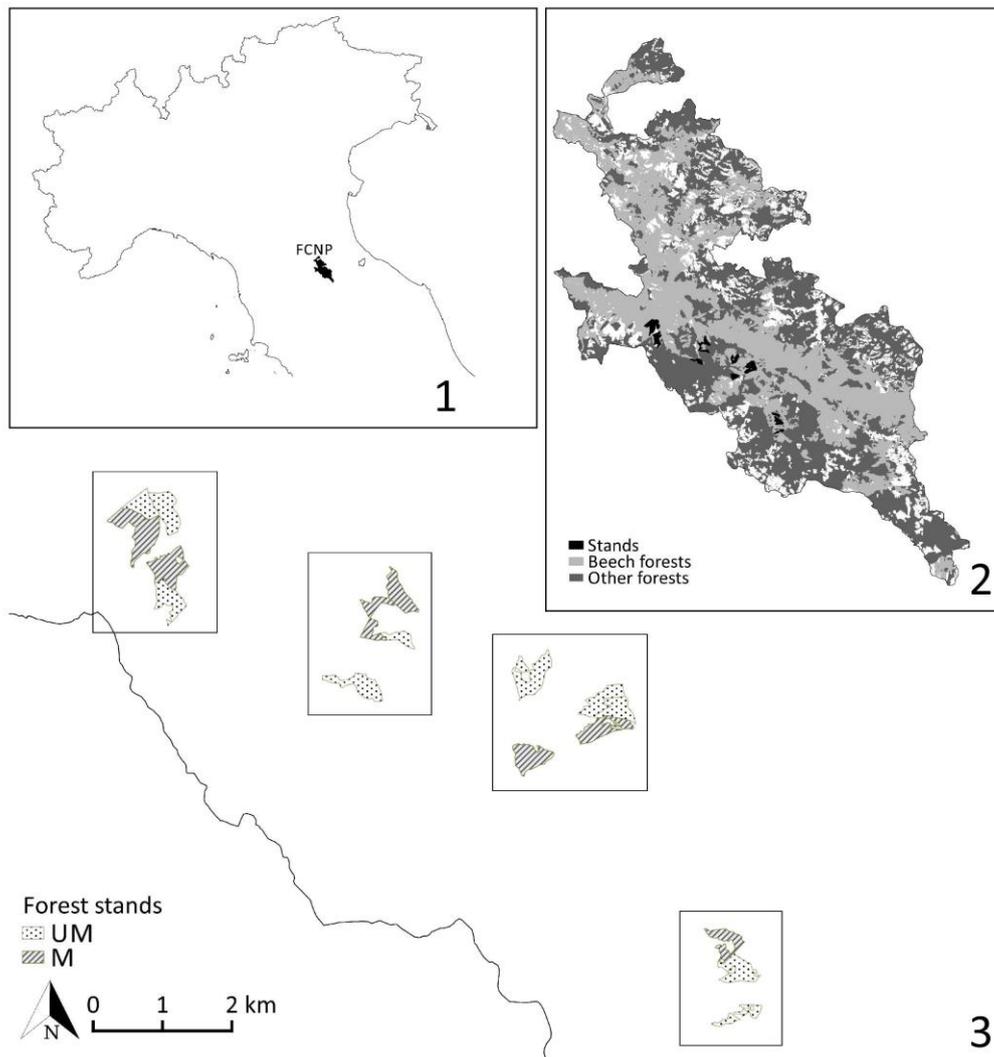


Figure 1 Location of the study area: (1) the Foreste Casentinesi National Park (FCNP) in the northern Apennines; (2) FCNP surface covered by forests (dark grey), by beech forests (light grey) and, among the latter, the stands selected for this study (black); 3) Managed (M) and Abandoned (UM) sampled stands are divided in four spatial clusters from North-West to South-East.

2.2 Sampling design

Sampling was designed to be balanced with respect to the two treatments (i.e., management vs. abandonment). We selected four spatial clusters, each one including presently managed (M), i.e., in conversion to high stands, and abandoned (UM) stands. The total number of stands was 20, ranging in size from 0.03 to 0.19 km² (mean = 0.12 km², standard deviation = 0.04). The use of clusters of M and UM stands permitted to minimize the environmental variability between the two treatments. Consequently, the M and UM treatments had a comparable range of topographical and climatic conditions. This sampling design was based on the Management Plan of the “Foreste Casentinesi” (Bresciani et al., 2008). All the stands had a same past history of coppicing according to the coppice

selection system, in which the coppice stand was organized into three age classes with shoots of different age and diameter coexisting on the same stool and an harvesting rotation period of 8 to 12-year rotation (Coppini and Hermanin, 2007). UM stands were abandoned during the '60s, while M stands underwent a planned conversion process to high forests that started with a gradual reduction of stem density. Field work was carried out during July 2017. For each stand a maximum of three sampling units (hereafter plots) were randomly located, for a total of 55 squared plots 20 m x 20 m. Plots were placed at a minimum distance of 200 m one to each other and more than 30 m far from the nearest stand edge. For seven small stands (area between 0.03 and 0.06 km²) it was not possible to locate three sampling units at the minimum distance, and they were sampled by one (4 stands) or two plots (3 stands) only. Each sampling unit consisted of a squared plot of 400 m² divided into four 10 m × 10 m subplots. The coordinates of the central point were recorded using a GPS device.

2.3 Species inventory

Each plot was divided in four subplots and the species occurrence of vascular plants was assessed within each subplot, resulting infrequency from 0 to 4). Plants were classified into two layers: herb layer (height < 1.30 m) and upper layer (including shrub and trees) (height \geq 1.30 m). The nomenclature of the species followed Conti et al. (2005).

Epiphytes were sampled on four trees for each plot, for a total of 220 trees, considering the most central tree of each subplot, with a DBH \geq 20 cm. The sampling unit used for epiphytes was a 20 cm x 160 cm (wide x high) plot named “ep-plot”, located on the tree trunk oriented northward. Only species occurrence was recorded within the plot. Nomenclature of lichen species followed Nimis (2016). Nomenclature of bryophytes followed Atherton et al. (2010), and Cortini Pedrotti (2006, 2010).

2.4 Structural and environmental features

Within each plot we measured the following structural attributes: i) DBH of each living stem with a minimum height threshold of 1.5 m, ii) tree height and canopy coverage of the four trees selected for the survey of epiphytes; this latter was estimated by a spherical densiometer oriented northward at the base of the four stems for each plot.

Environmental attributes of the plots were quantified by eight topographic and climatic variables: elevation (measured in m), slope (degrees), aspect (degrees), terrain roughness (calculated as the mean difference between a central pixel and its surrounding cells with a DEM with 20 m of spatial resolution), Topographic Wetness Index (TWI, which estimates the soil wetness based on the topography with a minimum of zero in plains), annual potential solar radiation ($W/m^2/year$), mean

annual rainfall (mm), mean annual temperature (°C). Topographic variables were derived from a digital elevation model (DEM) (Ispra, online resource). Roughness was measured by an index that considers differences in elevation across adjacent cells (Riley et al., 1999). The Topographic wetness index was calculated with the SAGA library in QGIS version 2.12 (QGIS Development Team, 2016). For computing the annual potential solar radiation we used the GRASS function “r.sun”, taking into account elevation, slope and aspect of each sampling point. Mean annual rainfall and temperature were obtained by spatial interpolation of the climatic stations available in the Tuscan Region, for the period 1995-2014, operated by Consorzio Lamma.

2.5 Data analysis

Firstly, we compared M and UM stands in terms of structural features. We quantified the structural features of each plot by eight variables: mean DBH (diameter at breast height), DBH diversity (Sabatini et al., 2015) calculated using the Gini-Simpson Index (function “diversity”, vegan R package, Oksanen et al., 2018), canopy closure, prevalent tree height (calculated as the mode), vertical heterogeneity calculated as the difference between the minimum and the maximum tree height, the tree density based on the number of shoots inventoried in each plot, the stand maturity, and the time from the last intervention. Tree ages and the time span from the last cut were derived from the Management Plan of the “Foreste Casentinesi” (Bresciani et al., 2008). The last cut was categorized into four levels (classes 1–4), representing different time spans of years, from recent to old harvests (< 3, 5-10, 10-20, > 50 years, respectively).

We tested for significant differences in topographical and structural variables between M and UM stands with the Mann-Whitney-Wilcoxon Test (R function “wilcox.test”).

Secondly, we compared the M and UM stands in term of species richness (mean species richness per plot, and total species richness per treatment) and composition of both epiphytes and vascular plants. For the vascular plants we analyzed the herb layer.

Third, we tested the effect of individual structural, topographical and climatic variables on the species composition of the three taxa. As response variables, we used the species occurrence at plot level by aggregating values of presence on each of the four subplots (for the herb layer), and on each of the four trees (for the epiphytes), with ranges of occurrence from 0 to 4. Using these data we performed PERMANOVA (Anderson, 2001) based on 9999 permutations (function “adonis”, vegan R package). For the explanatory variables, we reduced the redundancy among environmental and structural variables, respectively, analyzing their correlation (corrplot R package, Wei and Simko, 2017). Considering only the significant correlations (p-values < 0.01, Hmisc R package, Harrell et al., 2018), we used as threshold a correlation value of 0.5 to reduce the number of the

explanatory variables (structural and environmental attributes). Non-metric multidimensional scaling (NMDS) with function `metaMDS` (`vegan` R package) based on Bray–Curtis distance was then used to visualize the distribution of pools of species in relation to the environmental and structural variables that resulted significant in the models (Kumar et al., 2017). To underline ecological patterns in the species assemblages, we classified the vascular plants according to their habitat affiliation in two coarse classes: generalist species growing on a broad range of mountain forests and in clearings (Pignatti, 1982; Viciani et al., 2010), and “beech forest species” according to Willner et al. (2009). Lichens were classified according to the ecological indicator value for the pH of the substratum on which they usually grow (Nimis, 2016; Nimis and Martellos, 2017): generalist species growing on a wide range of substrata and specialist species growing on substrata from very acid (class 1) to subacid/subneutral (class 3). Bryophytes were classified for substratum and habitat affiliation according to Hill et al. (2007).

Finally, we performed an indicator species analysis (function `multipatt`, R package `Indicspecies`, De Cáceres and Jansen, 2016) with 9999 permutations, to evaluate the association of species with categorical factors (i.e., M and UM stands or harvesting periods) for which a significant difference in species composition was proved.

All the analyses were performed with the R statistical software version 3.4.2 (R Core Team, 2017).

3 Results

Overall, we recorded 113 species of vascular plants, 60 species of lichens and 17 species of bryophytes.

3.1 Managed vs. Abandoned stands

Structurally, M stands were characterized by higher DBH and tree height, while UM stands showed higher tree density, and a multi-layered canopy (i.e., vertical heterogeneity) (*Table 1*). The number of species per plot differed significantly between M and UM only for the vascular plants, with a higher values in the M plots, while the cumulative species richness per treatment was similar both for vascular plants and epiphytes (*Table 1*).

Table 1 Descriptive statistics: environmental and structural variables for each treatment (UM = abandoned stands; M = managed stands). Mean and standard deviation (mean \pm sd) were calculated on the data at stand level. DBH.mean = average trees DBH, DBH.div = DBH diversity, H.prev = prevalent height of the tree layer, VH = vertical heterogeneity of trees height, Age = stand maturity, SR = species richness.

		UM (stands=10, plots=28)	M (stands=10, plots=27)
Topography	Elevation (m a.s.l.)	1224.60 \pm 149.00	1276.76 \pm 99.81
	Slope (°)	25.20 \pm 8.70	20.33 \pm 7.61
	Aspect (°)	180.00 \pm 94.60	165.75 \pm 94.60
Forest structure	DBH.mean (cm) *	12.54 \pm 2.86	28.50 \pm 9.02
	DBH.div (cm) *	0.98 \pm 0.02	0.95 \pm 0.03
	H.prev (m)	18.42 \pm 3.66	20.92 \pm 3.20
	VH (m) *	14.00 \pm 3.75	2.85 \pm 3.56
	Canopy closure (%)	91.78 \pm 2.43	92.80 \pm 1.97
	Trees density (%) *	33.66 \pm 14.43	8.64 \pm 4.21
	Age (61-118 y)	82.10 \pm 14.13	82.90 \pm 10.13
Vascular plants (n = 113)	SR	86	86
	SR/plot *	8.90 \pm 4.74	13.83 \pm 7.70
Lichens (n = 60)	SR	53	50
	SR/plot	14.00 \pm 3.25	14.60 \pm 2.72
Bryophytes (n = 17)	SR	14	14
	SR/plot	4.05 \pm 1.57	4.62 \pm 1.32

*indicates significant differences (p-values < 0.05, Mann-Whitney-Wilcoxon Test)

Vascular plants showed a significant (p -value < 0.05) difference in species composition between M and UM treatments, with a significant effect also of the harvesting period (*Table 2*).

Table 2 Results of PERMANOVA analysis of compositional variability at plot scale. Abbreviations: DBH = mean DBH; Canopy = canopy closure; Age = stand maturity; Harv = harvesting period; TWI = Topographic Wetness Index; P = rainfall; T = temperature; Sun = solar radiation.

	Source	SS	MS	F	R ²	P
VASCULAR PLANTS	Structure					
	Treatment (M/UM)	0.67	0.67	2.27	0.03	0.010*
	DBH	0.52	0.52	1.77	0.03	0.031*
	Canopy	1.02	1.02	3.46	0.05	0.001*
	Age	0.32	0.32	1.08	0.02	0.323
	Harv	0.99	0.49	1.68	0.05	0.025*
	Topography					
	Slope	0.53	0.53	1.80	0.03	0.039*
	TWI	0.64	0.64	2.16	0.03	0.011*
	Climate					
	T	1.31	1.31	4.44	0.06	0.001*
	P	0.60	0.60	2.03	0.03	0.016*
	Sun	0.81	0.81	2.76	0.04	0.002*
	Residuals	12.65	0.29		0.63	
	Total	20.05			1.00	
	LICHENS	Structure				
Treatment (M/UM)		0.14	0.14	1.44	0.02	0.159
DBH		0.21	0.21	2.14	0.03	0.017*
Canopy		0.13	0.13	1.32	0.018	0.233
Age		0.21	0.21	2.16	0.03	0.023*
Harv		0.18	0.09	0.94	0.03	0.538
Topography						
Slope		0.15	0.15	1.58	0.02	0.095
TWI		0.16	0.16	1.66	0.023	0.077
Climate						
T		0.46	0.46	4.80	0.068	0.001*
P		0.76	0.76	7.83	0.11	0.001*
Sun		0.32	0.32	3.33	0.05	0.001*
Residuals		4.07	0.09		0.60	
Total		6.91			1.00	
BRYOPHYTES		Structure				
	Treatment (M/UM)	0.13	0.13	0.82	0.01	0.567
	DBH	0.16	0.16	1.07	0.02	0.389
	Canopy	0.47	0.47	3.05	0.05	0.010*
	Age	0.43	0.42	2.78	0.04	0.010*
	Harv	0.44	0.22	1.43	0.04	0.167
	Topography					
	Slope	0.23	0.23	1.47	0.02	0.202
	TWI	0.47	0.47	3.05	0.05	0.014*
	Climate					
	T	0.76	0.76	4.99	0.07	0.001*
	P	0.32	0.32	2.10	0.03	0.054
	Sun	0.36	0.36	2.36	0.03	0.045*
	Residuals	5.97	0.15		0.62	
	Total	10.10			1.00	

The most frequent species in the herb layer of the M stands were *Moehringia trinervia* (L.) Clairv. (63% of the plots), *Cardamine bulbifera* (L.) Crantz (63%), *Viola reichenbachiana* Jord. ex Boreau (55%), *Anemone nemorosa* L. (52%), *Festuca heterophylla* Lam. (52%), *Lactuca muralis* (L.) Gaertn. (52%), while the most frequent species in the UM stands were *Cytisus scoparius* (L.) Link (50%), *Festuca heterophylla* (43%), *Hieracium murorum* L. (39%), *Luzula nivea* (L.) DC. (39%), *Moehringia trinervia* (32% of the plots), *Viola reichenbachiana* (32%). A number of species only occurred as unique in each treatment.

With the indicator species analysis (Table 3), a group of 10 species of vascular plants was associated to the M stands with (p-value < 0.05), while none of the species showed to be indicative exclusively of the UM stands. Most of the species associated to M stands grow in a wide range of mountain, mostly broadleaved, forests and in clearings (*Lactuca muralis*, *Rubus idaeus* L., *Rubus hirtus* Waldst. & Kit., *Senecio ovatus* (P. Gaertn., B. Mey. & Scherb.) Willd., *Alliaria petiolata* (M. Bieb.) Cavara & Grande, *Fragaria vesca* L.), or can live also in open and disturbed habitats (*Hypericum perforatum* L., *Silene dioica* (L.) Clairv., *Rumex acetosella* L.), while only one species (*Carex sylvatica* Huds.) is listed as “beech forest species” (i.e., with high fidelity to beech forests).

Table 3 Species of vascular plants with a significant indicator value for treatment (M/UM).

Species	Indicator value
Managed stands	
<i>Lactuca muralis</i>	0.002
<i>Rubus idaeus</i>	0.040
<i>Rubus hirtus</i>	0.027
<i>Senecio ovatus</i>	0.008
<i>Carex sylvatica</i>	0.017
<i>Silene dioica</i>	0.008
<i>Hypericum perforatum</i>	0.028
<i>Alliaria petiolata</i>	0.049
<i>Rumex acetosella</i>	0.046
<i>Fragaria vesca</i>	0.033

Species typical of clearings or disturbed habitats were also indicative of the three most recent harvesting periods (Table 4).

Table 4 Species of vascular plants with a significant indicator value for harvesting periods from recent to old interventions (< 3, 5–10, 10–20, > 50 years, respectively).

Species	Indicator value	Species	Indicator value
< 3 years		< 3 and 5-10 years	
<i>Senecio ovatus</i>	0.001	<i>Lactuca muralis</i>	0.001
<i>Carex spicata</i>	0.003	<i>Cytisus scoparius</i>	0.003
<i>Prenanthes purpurea</i>	0.004	<i>Rubus hirtus</i>	0.008
<i>Galium aristatum</i>	0.007	<i>Veronica officinalis</i>	0.032
5-10 years		<i>Senecio aquaticus</i>	0.012
<i>Fragaria vesca</i>	0.005	<i>Silene dioica</i>	0.038
<i>Carex sylvatica</i>	0.014	<i>Hypericum perforatum</i>	0.033
<i>Malva moschata</i>	0.037	< 3, 5-10, and 10-20 years	
<i>Senecio squalidus</i>	0.035	<i>Moehringia trinervia</i>	0.008
		<i>Cardamine bulbifera</i>	0.013

For both epiphytic lichens and bryophytes differences in species composition between M and UM stands were not significant. Overall, the most frequent lichens were: *Phlyctis argena* (Spreng.) Flot. (100% of the plots), *Melanelixia glabratula* (Lamy) Sandler & Arup (91%), *Arthonia radiata* (Pers.) Ach. (87%), *Parmelia saxatilis* (L.) Ach. (82%), *Buellia griseovirens* (Sm.) Almb. (80%), *Parmelia sulcata* Taylor (80%); 12 species (20%) occurred only once. Most of the sampled lichens are very spread in Italy and generalists for habitat affiliation, while only two species have a high fidelity to beech forests (*Arthonia didyma* Körb., *Parmelia submontana* Hale). For the bryophytes,

only 7 species occurred in more than 5 plots, with all the other being unfrequent. The most abundant species were: *Hypnum cupressiforme* Hedw. (84%), *Pterigynandrum filiforme* Hedw. (67%), *Radula complanata* (L.) Dumort. (65%), *Frullania dilatata* (L.) Dumort. (55%), *Brachythecium velutinum* W.P.Schimper (33%), *Orthotrichum striatum* Hedw. (31%); 4 species (24%) occurred only once. All the sampled bryophytes are generalist for substratum and habitat affiliation, and able to grow on a wide spectrum of different substrata (mostly rocks and barks) and habitats (e.g., most of the species can live in sparsely wooded grasslands, included parklands, in hedgerows, or in broadleaved deciduous woodlands).

3.2 Effect of topography, climate and forest structure on species composition

The reduction of the environmental variables used to analyze species composition resulted into the selection of i) mean annual temperature (negatively related to the elevation and longitude and positively related to latitude), ii) mean annual rainfall (negatively related to the elevation and longitude, and positively related to latitude), iii) TWI (negatively related to the terrain roughness), iv) slope (positively related to the terrain roughness), and v) potential mean annual solar radiation (*Figure 2*). Accordingly, the reduction of the structural variables resulted into the selection of: i) mean DBH (negatively related to the tree density, DBH diversity, and vertical heterogeneity), ii) stand maturity (positively related to the prevalent tree height), and iii) canopy closure (*Figure 2*).

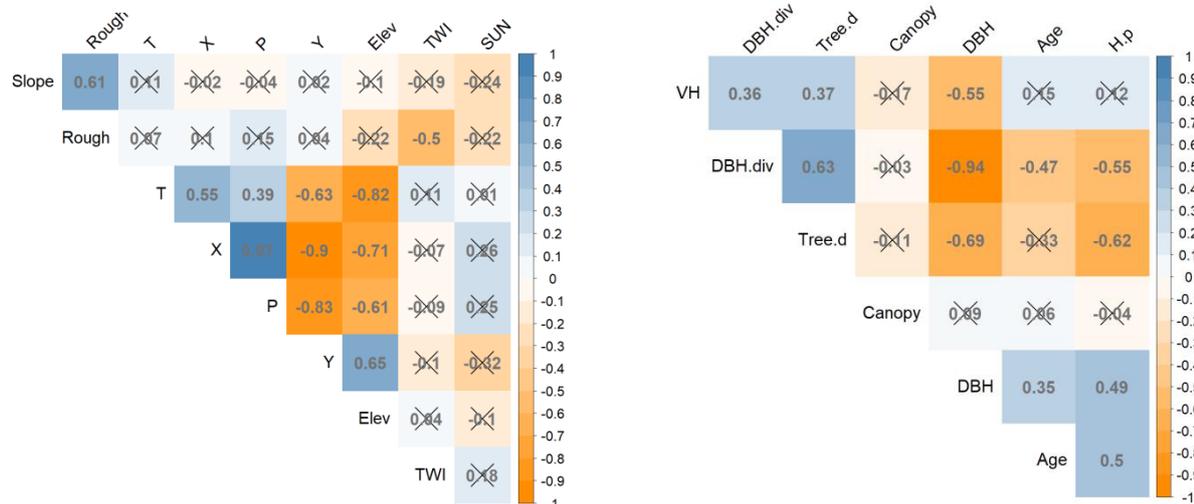


Figure 2 Correlation values for environmental and structural variables, respectively. Data are referred to plot level. P-values < 0.01 for not crossed-out correlations. Blue and orange values indicate positive and negative correlations, respectively. Environmental variables: Elev = elevation, TWI = Topographic Wetness Index, SUN = annual solar radiation, Rough = terrain roughness, T = mean annual temperature, P = mean annual rainfall, X = longitude, Y = latitude. Structural variables: Age = stand maturity, DBH = average trees DBH, H.p = prevalent height of the tree layer, Canopy = percentage of canopy closure, DBH.d = DBH diversity, Tree.d = density of trees (percentage), VH = vertical heterogeneity.

Topographic and climatic variables significantly modified the occurrence of different species of vascular plants, while among the structural variables canopy coverage and the average DBH were significant (Table 2). NMDS ordination performed on vascular plants species composition showed a prevalence of beech forest species with increasing the canopy closure and the mean DBH (Figure 3). On the contrary, changes in topographic and climatic variables were mostly related to changes in the occurrence of generalist species (Figure 3).

The composition of epiphytic lichens was influenced by climatic variables, and by structural variables, that is the mean DBH and the maturity of forest stands. With increasing stand maturity, mean DBH and rainfalls, the occurrence of species living on substrata from very acid to subacid increased, while changes in temperature and solar radiation influenced mostly the occurrence of species living on subacid, subneutral substrates as well as species living on a wider range of substratum pH (from acid to basic) (Figure 3).

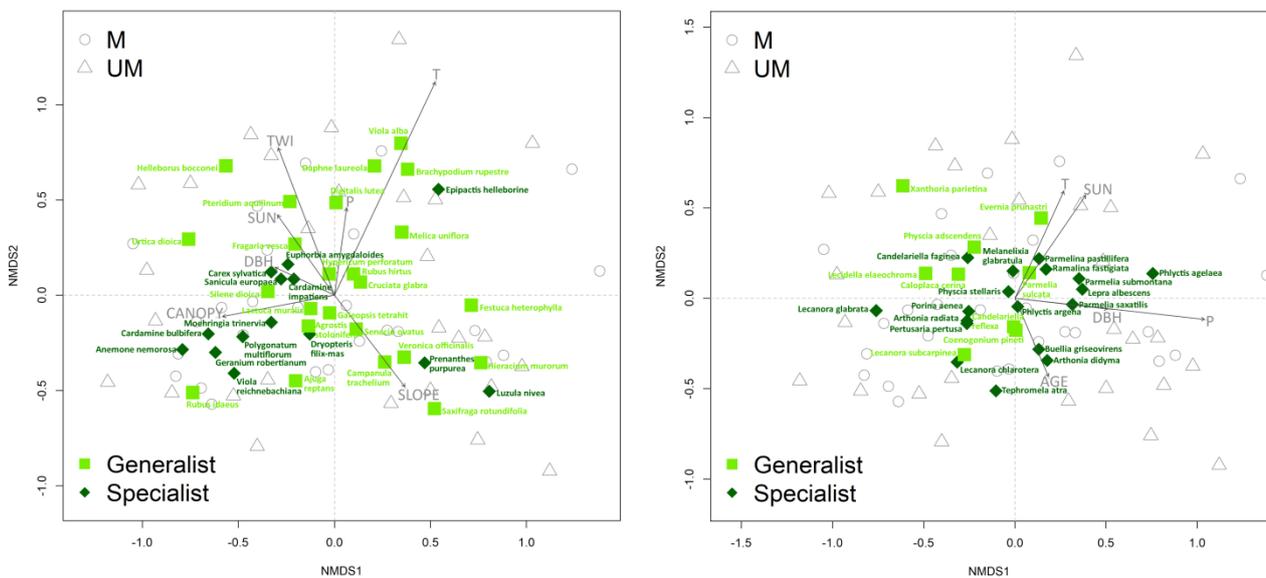


Figure 3 NMDS ordination performed on the vascular plants of the herb layer (left) and lichens (right). Only species occurring in ≥ 5 plots are shown. Vascular plants are grouped according to their habitat affiliation: Specialist = beech forest species (*sensu* Willner et al. 2009); Generalist = species which grow in forest clearings and in a broader range of mountain, mostly broadleaved, forests. Lichens are classified in two groups according to the ecological indicator value for the pH of substratum: Specialist = species living on substrata from very acid (class 1) to subacid/subneutral (class 3); Generalist = species living on a broad range of substratum pH. M = Managed stands; UM = Abandoned stands.

Species composition of bryophytes was influenced by changes in the climatic conditions, as well as by structural variables likely influencing microclimate: light conditions (solar radiation, canopy closure), temperature and humidity (TWI) (Table 2). As for lichens, the effect of stand maturity was also significant. However, we recorded few species of bryophytes all generalist for habitat affiliation, and we did not identify a particular ecological pattern in the occurrence of the species, contrary to vascular plants and lichens.

4 Discussion

The abandonment of forest management practices dating back 60-70 years ago is still not sufficient to evidence clear differences in species richness and composition of the epiphytes in the mountain beech forest here investigated, while vascular plants showed an already evident response. Further, irrespective of management or abandonment, conservation actions should take into account that more than topography and climate, suitable habitat structures are key for the occurrence of specialist species in the investigated mountain beech forests.

4.1 Management vs. Abandonment

In a relatively short time after withdrawal from management (60-70 years), differences between abandoned and managed mountain beech forest stands were reflected by changes in the assemblages of vascular plants, without significant response of the epiphytic lichens and bryophytes, thus showing contrasting results among these species groups (e.g., Chiarucci et al., 2007). Previous studies showed that vascular plants, including typical forest species, can benefit from the resource increase (e.g., light and nutrients) resulting from moderate management disturbance (Roberts, 2004; Boch et al., 2013). In our study, we found that the managed stands were characterized by the occurrence of vascular plants with more variable ecological requirements as compared to the abandoned stands. The conversion into high forest, with a gradual thinning of the canopy, likely generates a variability of micro-environmental conditions (i.e., light, humidity) within the stand, thus promoting even light-demanding species typically growing in clearings and forest edges. This is usually directly associated to the lower, and more heterogeneous, canopy closure of managed stands than of the abandoned ones (e.g., Scolastri et al., 2016), that was, however, not significantly different between managed and abandoned stands in our study. Nevertheless, this contrasting result can suggest that, besides the sole degree of canopy closure, other factors more strongly control the quality of light, and especially the PAR (Photosynthetic Active Radiation), transmitted through the canopy. In fact, shifts in the understory light environment due to changes in forest structure and vertical arrangement of leaves and stems can be more relevant in creating differences in light regime than is the sheer amount of canopy area or biomass (Brown and Parker, 1994). The more homogeneous conditions of the abandoned stands may reflect their age – still young – and a still strong legacy with the past management (Schall et al., 2018), without reaching yet natural levels of habitat heterogeneity. Structure, processes and natural disturbance events which may increase habitat heterogeneity and the resource availability for several species groups in old-growth forests, may still be not evident in many abandoned forests in Europe (Burrascano et al., 2017; Sabatini et al., 2018; Schall et al., 2018). Indeed, old-growth

forests with a multi-layered canopy and natural gaps are characterized by a fine-grained structure in the herb layer with small species-rich patches, precisely due to heterogeneous light conditions (Standovár et al., 2006; Brunet et al., 2010). Accordingly, the lack of significant differences in species assemblages for the epiphytes is likely due to a, still, little structural differentiation among managed and abandoned stands. Notably, especially for epiphytes of conservation concern, the presence of specific structural attributes (i.e., old, damaged beech trees), has been identified in several studies as key for their occurrence (e.g., Fritz et al., 2009; Fritz and Brunet, 2010), but these attributes were lacking in our study system, even in the abandoned forests.

4.2 Effects of structure, topography and climate in shaping species assemblages

Irrespective of management or abandonment, in our study structural features played a major role in driving specific assemblages of specialized species. Notably, vascular plants with their ecological optima in beech forests (“beech forest species” *sensu* Willner et al., 2009), which are typically described as adapted to mesic conditions and shade-tolerant, were favored by the increase of canopy closure and stem size. These factors are physically correlated to changes in moisture and temperature regimes (Krah et al., 2018). Changes in microclimatic conditions, likely even linked to structure (especially canopy closure in this case) significantly influenced also the assemblages of epiphytic bryophytes. The continuity of forest microclimate (high and balanced air humidity) has been assessed in previous studies as one of the most relevant drivers of forest dwelling bryophytes (Standovár et al., 2006; Ódor et al., 2014). However, we stress that for the bryophytes we had only a spotty view of the drivers which shape their assemblages, given the low number of recorded species, all highly generalists for substratum and habitat affiliation.

Epiphytic lichens responded to contrasting factors as compared to vascular plants and bryophytes. In our analyses, a major determinant for the diversity of lichens assemblages was the climate, that play a relevant role, as it is already recognized (Nascimbene et al., 2014). However, the importance of host tree species in driving lichen patterns often overrides that of stand level factors indicative of forest structure and climate (Nascimbene et al., 2013b). Many studies have emphasized that different epiphytic assemblages are linked to different chemical-physical features of the bark (e.g., Fritz et al., 2008; Fritz, 2009; Ódor et al., 2014). Indeed, we found lichens with an affiliation for substrata from very acid to sub-acid at increasing stem size and mean annual rainfall. We observed the same trend at increasing the stand maturity, while, on the contrary, species more generalist, in terms of substratum pH, decreased. These findings may be associated to the low buffering capacity of the beech bark with a concurrent acid stemflow which could result in acidification of large stem areas, while beech growth generates hydrogen ions that lower the pH (Fritz et al., 2009).

4.3 Management implications

Different taxonomic groups exhibit different rates of recovery over time (Nascimbene et al., 2013a; Spake et al., 2015) and the effect of management cessation where the legacy of past management is still detectable in the forest structure may change in the long term when natural disturbances increase the attributes of old-growth forests (Kaufmann et al., 2017; Nascimbene et al., 2013a). This can explain our overall results, with an effect of 60-70 years of abandonment of forest practices that is yet not detectable in the response of the forest dwellers, especially epiphytes. For instance, many comparative studies showed that the observed higher diversity of bryophytes in old-growth stands is boosted by the higher amount of potential substrates (i.e., deadwood) as compared with managed stands (Standovár et al., 2006), that we did not analyze since its amount was still very low even in the abandoned stands. Further, the lack of epiphytic specialist species, as well as the absence of species of conservation concern, is most likely due to the lack of the required structural attributes (Fritz et al. 2008; Fritz and Brunet, 2010; Nascimbene et al., 2013b).

Therefore, to increase the conservation values of forests, and to reach overall forest biodiversity conservation goals, a strategy based on integrative and segregative approaches is suggested (Kraus and Krumm, 2013), with reservation, retention, and restoration of old-growth forest attributes (Bauhus et al., 2009), and with actions not limited to the stand scale (Schall et al., 2018). In this perspective, a network of set-aside areas (i.e., reservation) may act as shelter and propagation node for forest species, integrated within a network of key habitats at smaller spatial scale, such as retention groups of old and damaged trees, and a suitable matrix that allows good dispersal to the set-asides, but also provides habitat in itself for many species (Vandekerckhove et al., 2013 in Kraus and Krumm, 2013). However, the retention and restoration of suitable habitats may not be enough for ensuring the presence of dispersal-limited species previously disappeared because of lacking of suitable conditions (e.g., Hedin et al. 2008; Ellis, 2012; Nascimbene et al., 2013b). Indeed, species associated with old-growth attributes may be restricted to relict areas because of their poor dispersal capacity (e.g., Öckinger et al. 2005). Therefore, even active interventions, such as transplants of lichens in retained or restored tree habitats (Öckinger et al., 2005; Jüriado et al., 2011), may be recommended for enhancing the conservation values of forest patches, especially in areas far from source-populations.

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References

- Anderson, M.J. (2001). A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46. <https://doi.org/10.1111/j.1442-9993.2001.01070.pp.x>
- Atherton, I., Bosanquet, S., Lawley, M. (2010). *Mosses and Liverworts of Great Britain and Ireland – a field guide.* British Bryological Society & Latimer Trend & Co. Ltd, Plymouth.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manage.* 258, 525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>
- Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A., Hessenmöller, D., Kalko, E.K.V., Linsenmair, K.E., Pfeiffer, S., Pommer, U., Schöning, I., Schulze, E.D., Seilwinder, C., Weisser, W.W., Wells, K., Fischer, M., 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. *Basic Appl. Ecol.* 14, 496–505. <https://doi.org/10.1016/j.baae.2013.06.001>
- Bresciani, A., Borchi, S., Chiccioli, P., Fantoni, I., Nicoloso, S., 2008. Il piano di gestione del complesso regionale Foreste Casentinesi (AR): la selvicoltura quale strumento di realizzazione delle finalità del Parco nazionale. III Congresso Nazionale di Selvicoltura 109–115.
- Brown, M.J., Parker, G.G., 1994. Canopy light transmittance in a chronosequence of mixed-species deciduous forests. *Can. J. Forest Res.* 24, 1694–1703. <https://doi.org/10.1139/x94-219>
- Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. *Ecol. Bull.* 53, 77–94. <https://doi.org/10.1016/j.jnc.2017.08.001>
- Burrascano, S., Keeton, W.S., Sabatini, F.M., Blasi, C., 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *For. Ecol. Manage.* 291, 458–479. <https://doi.org/10.1016/j.foreco.2012.11.020>
- Burrascano, S., Ripullone, F., Bernardo, L., Borghetti, M., Carli, E., Colangelo, M., Gangale, C., Gargano, D., Gentilella, T., Luzzi, G., Passalacqua, N., Pelle, L., Rivelli, A.R., Sabatini, F.M., Schettino, A., Siclari, A., Uzunov, D., Blasi, C., 2017. It's a long way to the top: Plant species diversity in the transition from managed to old-growth forests. *J. Veg. Sci.* 98–109. <https://doi.org/10.1111/jvs.12588>
- Campetella, G., Canullo, R., Gimona, A., Garadnai, J., Chiarucci, A., Giorgini, D., Angelini, E., Cervellini, M., Chelli, S., Bartha, S., 2016. Scale-dependent effects of coppicing on the species pool of late successional beech forests in the central Apennines, Italy. *Appl. Veg. Sci.* 19, 474–485. <https://doi.org/10.1111/avsc.12235>
- Chiarucci, A., D'Auria, F., Bonini, I., 2007. Is vascular plant species diversity a predictor of bryophyte species diversity in Mediterranean forests? *Biodivers. Conserv.* 16, 525–545. <https://doi.org/10.1007/s10531-006-6733-1>
- Consorzio Lamma, 2018. Climatic data for Tuscany. Retrieved from: <http://dati.lamma.toscana.it/group/clima-ed-energia> (accessed 8 January 2019).
- Conti, F., Abbate, G., Alessandrini, A., Blasi, C. (Eds.), 2005. *An Annotated Checklist of the Italian Vascular Flora.* Palombi, Rome.
- Coppini, M., Hermanin, L., 2007. Restoration of selective beech coppices: A case study in the Apennines (Italy). *For. Ecol. Manage.* 249, 18–27. <https://doi.org/10.1016/j.foreco.2007.04.035>
- Cortini Pedrotti, C., 2001. *Flora dei Muschi d'Italia I (Moss Flora of Italy I).* Antonio Delfino Ed., Rome.
- Cortini Pedrotti, C., 2006. *Flora dei Muschi d'Italia II (Moss Flora of Italy II).* Antonio Delfino Ed., Rome.
- De Cáceres, M., Jansen, F., 2016. Package “indicspecies” (Version 1.7.6). Retrieved from: <https://cran.r-project.org/web/packages/indicspecies/indicspecies.pdf> (accessed 8 January 2019).
- Ellis, C.J., 2012. Lichen epiphyte diversity: A species, community and trait-based review. *Perspect. Plant Ecol. Evol. Syst.* 14, 131–152. <https://doi.org/10.1016/j.ppees.2011.10.001>
- Fritz, Ö., Niklasson, M., & Churski, M., 2008. Tree Age is a Key Factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Appl. Veg. Sci.* 12, 93–106. <https://doi.org/10.1111/j.1654-109X.2009.01007.x>

- Fritz, Ö., 2009. Vertical distribution of epiphytic bryophytes and lichens emphasizes the importance of old beeches in conservation. *Biodivers. Conserv.* 18, 289–304. <https://doi.org/10.1007/s10531-008-9483-4>
- Fritz, Ö., Brunet, J., Caldiz, M., 2009. Interacting effects of tree characteristics on the occurrence of rare epiphytes in a Swedish beech forest area. *The Bryologist* 112, 488–505. <https://doi.org/10.1639/0007-2745-112.3.488>
- Fritz, Ö., Brunet, J., 2010. Epiphytic bryophytes and lichens in Swedish beech forests – effects of forest history and habitat quality. *Ecol. Bull.* 53, 95–107.
- Geoportale nazionale, 2018. Geological map of Italy. Retrieved from: <http://www.pcn.minambiente.it/mattm/> (accessed 8 January 2019).
- Harrell, F.E., 2018. Hmisc: Harrell Miscellaneous. R package version 4.1-1. Retrieved from: <https://CRAN.R-project.org/package=Hmisc> (accessed 8 January 2019).
- Hedin, J., Ranius, T., Nilsson, S. and Smith, H., 2008. Restricted dispersal in a flying beetle assessed by telemetry. *Biodivers. Conserv.* 17, 675–684. <https://doi.org/10.1007/s10531-007-9299-7>
- Hill, M.O., Preston, C.D., Bosanquet, S.D.S., Roy, D.B., 2007. BRYOATT: Attributes of British and Irish Bryophytes. Cambridge, Centre for Ecology and Hydrology.
- Janssen, P., Fuhr, M., Bouget, C., 2018. Small variations in climate and soil conditions may have greater influence on multitaxon species occurrences than past and present human activities in temperate mountain forests. *Divers. Distrib.* 1–14. <https://doi.org/10.1111/ddi.12705>
- Jüriado, I., Liira, J., Csencsics, D., Widmer, I., Adolf, C., Kohv, K., Scheidegger, C., 2011. Dispersal ecology of the endangered woodland lichen *Lobaria pulmonaria* in managed hemiboreal forest landscape. *Biodivers. Conserv.* 20, 1803–1819. <https://doi.org/10.1007/s10531-011-0062-8>
- Kaufmann, S., Hauck, M., Leuschner, C., 2017. Comparing the plant diversity of paired beech primeval and production forests: Management reduces cryptogam, but not vascular plant species richness. *For. Ecol. Manage.* 400, 58–67. <https://doi.org/10.1016/j.foreco.2017.05.043>
- Krah, F.S., Seibold, S., Brandl, R., Baldrian, P., Müller, J., Bässler, C., 2018. Independent effects of host and environment on the diversity of wood-inhabiting fungi. *J. Ecol.*, 1–15.
- Kraus, D., Krumm, F., 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity, European Forest Institute.
- Kumar, P., Chen, H.Y.H., Thomas, S.C., Shahi, C., 2017. Effects of coarse woody debris on plant and lichen species composition in boreal forests. *J. Veg. Sci.* 28, 389–400. <https://doi.org/10.1111/jvs.12485>
- Leuschner, C., Meier, I.C., Hertel, D., 2006. On the niche breadth of *Fagus sylvatica*: soil nutrient status in 50 Central European beech stands on a broad range of bedrock types. *Ann. For. Sci.* 63, 355–368. <https://doi.org/10.1051/forest:2006016>
- Nascimbene, J., Dainese, M., Sitzia, T., 2013a. Contrasting responses of epiphytic and dead wood-dwelling lichen diversity to forest management abandonment in silver fir mature woodlands. *For. Ecol. Manage.* 289, 325–332. <https://doi.org/10.1016/j.foreco.2012.10.052>
- Nascimbene, J., Thor, G., Nimis, P.L., 2013b. Effects of forest management on epiphytic lichens in temperate deciduous forests of Europe - A review. *For. Ecol. Manage.* 298, 27–38. <https://doi.org/10.1016/j.foreco.2013.03.008>
- Nascimbene, J., Nimis, P.L., Dainese, M., 2014. Epiphytic lichen conservation in the Italian Alps: The role of forest type. *Fungal Ecol.* 11, 164–172. <https://doi.org/10.1016/j.funeco.2014.06.006>
- Nimis P.L., 2016. The Lichens of Italy. A Second Annotated Catalogue. EUT, Trieste, 739 pp.
- Nimis P.L., Martellos S., 2017. ITALIC - The Information System on Italian Lichens. Version 5.0. University of Trieste, Dept. of Biology. Retrieved from: <http://dryades.units.it/italic> (accessed 8 January 2019).
- Nocentini, S., 2009. Structure and management of beech (*Fagus sylvatica* L.) forests in Italy. *iForest - Biogeosciences For.* 105–113. <https://doi.org/10.3832/ifor0499-002>
- Öckinger, E., Niklasson, M., Nilsson, S.G., 2005. Is local distribution of the epiphytic lichen *Lobaria pulmonaria* limited by dispersal capacity or habitat quality? *Biodivers. Conserv.* 14, 759–773. <https://doi.org/10.1007/s10531-004-4535-x>
- Ódor, P., Király, I., Tinya, F., Bortignon, F., Nascimbene, J., 2014. Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests. *For. Ecol. Manage.* 321, 42–51. <https://doi.org/10.1016/j.foreco.2014.01.035>
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2018. Vegan: community ecology package. Version 2.4-5. Retrieved from <https://cran.r-project.org/web/packages/vegan/index.html> (accessed 8 January 2019).
- Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.T., Schmidt, W., Standovár, T., Tothmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conserv. Biol.* 24, 101–112. <https://doi.org/10.1111/j.1523-1739.2009.01399.x>
- Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., 2015. Quantifying the recovery of

- old-growth attributes in forest reserves: A first reference for France. *For. Ecol. Manage.* 346, 51–64. <https://doi.org/10.1016/j.foreco.2015.02.037>
- Pignatti S., 1982. *Flora d'Italia*. Edagricole, Bologna.
- QGIS Development Team, 2016. QGIS Geographic Information System. Open Source Geospatial Foundation Project. Retrieved from <http://qgis.osgeo.org> (accessed 8 January 2019).
- R Core Team, 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Retrieved from: <https://www.R-project.org/> (accessed 8 January 2019).
- Riley, S.J., DeGloria, S.D., Elliot, R., 1999. A Terrain Ruggedness Index that Quantifies Topographic Heterogeneity. *Intermt. J. Sci.* 5, 23–27. <https://doi.org/citeulike-article-id:8858430>
- Roberts, M. R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Can. J. Botany*, 82, 1273–1283. <https://doi.org/10.1139/b04-091>
- Sabatini, F.M., Burrascano, S., Lombardi, F., Chirici, G., Blasi, C., 2015. An index of structural complexity for apennine beech forests. *IForest* 8, 314–323. <https://doi.org/10.3832/ifor1160-007>
- Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Duarte, I.M., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O.-P., Volosyanchuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2018. Where are Europe's last primary forests? *Divers. Distrib.* 1–14. <https://doi.org/10.1111/ddi.12778>
- Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Schulze, E.D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T., Ammer, C., 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *J. Appl. Ecol.* 55, 267–278. <https://doi.org/10.1111/1365-2664.12950>
- Scolastri, A., Cancellieri, L., Iocchi, M., Cutini, M., 2016. Old Coppice vs High Forest: the impact of beech forest management on plant species diversity in central Apennines (Italy). *J. Plant Ecol.* 1–10. <https://doi.org/10.1093/jpe/rtw034>
- Scolastri, A., Bricca, A., Cancellieri, L., Cutini, M., 2017. Understorey functional response to different management strategies in Mediterranean beech forests (central Apennines, Italy). *For. Ecol. Manage.* 400, 665–676. <https://doi.org/10.1016/j.foreco.2017.06.049>
- Sitzia, T., Semenzato, P., Trentanovi, G., 2010. Natural reforestation is changing spatial patterns of rural mountain and hill landscapes: a global overview. *For. Ecol. Manage.* 259, 1354–62. <https://doi.org/10.1016/j.foreco.2010.01.048>
- Sitzia, T., Campagnaro, T., Gatti, E., Sommacal, M., Kotze, D.J., 2015. Wildlife conservation through forestry abandonment: Responses of beetle communities to habitat change in the Eastern Alps. *Eur. J. For. Res.* 134, 511–524. <https://doi.org/10.1007/s10342-015-0868-0>
- Spake, R., Ezard, T.H.G., Martin, P.A., Newton, A.C., Doncaster, C.P., 2015. A meta-analysis of functional group responses to forest recovery outside of the tropics. *Conserv. Biol.* 29, 1695–1703. DOI: 10.1111/cobi.12548
- Standovár, T., Ódor, P., Aszalós, R., Gálhidy, L., 2006. Sensitivity of ground layer vegetation diversity descriptors in indicating forest naturalness. *Community Ecol.* 7, 199–209. <https://doi.org/10.1556/ComEc.7.2006.2.7>
- Vacchiano, G., Garbarino, M., Lingua, E., Motta, R., 2017. Forest dynamics and disturbance regimes in the Italian Apennines. *For. Ecol. Manage.* 388, 57–66. <https://doi.org/10.1016/j.foreco.2016.10.033>
- Vandekerkhove, K., De Keersmaeker, L., Menke, N., Meyer, P., Verschelde, P., 2009. When nature takes over from man: Dead wood accumulation in previously managed oak and beech woodlands in North-western and Central Europe. *For. Ecol. Manage.* 258, 425–435. <https://doi.org/10.1016/j.foreco.2009.01.055>
- Vandekerkhove K., Thomaes A., Jonsson B.-G., 2013. Connectivity and fragmentation: island biogeography and metapopulation applied to old-growth elements. In: Kraus, D., Krumm, F., 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity, European Forest Institute.
- Viciani, D., Agostini, N., 2008. La carta della vegetazione del Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna (Appennino Tosco-Romagnolo): note illustrative. *Quad. di Stud. e Not. di Stor. Nat. della Romagna* 97–134.
- Viciani, D., Gonnelli, V., Sirotti, M., Agostini, N., 2010. An annotated check-list of the vascular flora of the “Parco Nazionale delle Foreste Casentinesi, Monte Falterona e Campigna” (Northern Apennines Central Italy). *Webbia* 65, 3–131. <https://doi.org/10.1080/00837792.2010.10670867>
- Wei T., Simko V., 2017. R package "corrplot": Visualization of a Correlation Matrix (Version 0.84). Retrieved from <https://github.com/taiyun/corrplot/> (accessed 8 January 2019).
- Willner, W., Di Pietro, R., Bergmeier, E., 2009. Phylogeographical evidence for post-glacial dispersal limitation of European beech forest species. *Ecography (Cop.)*. 32, 1011–1018. <https://doi.org/10.1111/j.1600-0587.2009.05957.x>

CHAPTER V

Biodiversity response to forest structure and management: Comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation

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ABSTRACT

Aim: We investigated the consistency between richness and trait-based diversity metrics in capturing the effects of management-related habitat factors on biodiversity. The choice of biodiversity metrics can substantially affect the evaluation of conservation tools. However, the relative sensitivity of different metrics is not well investigated, especially in a multi-taxon framework.

Location: European beech forests in Denmark.

Methods: We studied 20 beech stands comprising four management types (from intensively managed to long unmanaged stands). We analyzed how management-related environmental variables were reflected in the measure of: (i) species richness, (ii) number of conservation-relevant species (red-listed species and old-growth forest indicators) and (iii) functional diversity targeting five organism groups with different habitat requirements, i.e. vascular plants, epiphytic lichens and bryophytes, saproxylic fungi and breeding birds.

Results: Plain species richness at stand level was generally misleading, as it did not capture changes in the number of conservation relevant species with changes in management-related environmental variables. The interpretation of functional responses was most informative for the better known vascular plants, while responses were more fragmented for the other organism groups. Overall, however, functional responses were consistent with a loss of specialization and progressive simplification of species assemblages from long-unmanaged to intensively managed stands.

Conclusions: Our findings suggest that the occurrence of conservation-relevant species is a sound and relevant metric for planning and evaluating conservation actions, especially for less studied organism groups (e.g., saproxylic fungi and epiphytes). The functional approach is promising, but presupposes the availability of databases of relevant traits.

Key-words: European beech forests; Birds; Community-weighted mean; Epiphytes; GLMM; Habitat structure; Multi-taxon biodiversity; Rao's quadratic diversity; Vascular plants; Wood-inhabiting fungi.

<i>Contents</i>	<i>page</i>
1 Introduction	81
2 Materials and methods	83
2.1 Study area	83
2.2 Data collection	84
2.3 Functional traits	86
2.4 Data analysis	88
3 Results	90
4 Discussion	94
4.1 Species richness	94
4.2 Functional diversity	96
5 Conclusions	98
Author Contributions	99
Aknowledgements	99
Funding	99
References	99

1 Introduction

European beech forest is a fundamental type of natural vegetation in temperate Europe (Brunet et al., 2010). However, a long history of human use including modern forestry (Bengtsson et al., 2000) has led to substantial habitat loss and changes in forest structure and dynamics (e.g., Paillet et al., 2010; Burrascano et al., 2013). Human intervention has generated a simplification of forest ecosystems, with a consequent decrease of several sensitive and narrow-range species depending on structures and processes of old-growth forests (e.g., Brunet et al., 2010; Paillet et al., 2010; Sabatini et al., 2018). For instance, certain epiphytic bryophytes and lichens, which inhabit old and damaged trees, are threatened due to the removal of their habitat trees in production forests (Fritz and Brunet, 2010). To counteract biodiversity loss, various measures have been suggested, spanning from the segregation of non-intervention forest reserves to the integration of wildlife-friendly elements, such as leaving retention trees and dead wood to support habitat specialists, in so-called “near-natural” forestry (Bauhus et al., 2009). While forest reserves represent a land-sparing approach, “near-natural” forestry is cognizant with a land-sharing philosophy, resting on the assumption that silviculture can be optimized to protect most forest biodiversity without major consequences for economic outcomes. However, knowledge of the impacts of “near-natural” forestry on biodiversity is limited in the temperate zone. Therefore it is debated how the two approaches can be combined and balanced to provide cost-effective conservation (Kraus and Krumm, 2013).

So far, the effects of management on biodiversity have been investigated mostly with a focus on stand-level **species richness** (Paillet et al., 2010; Chaudhary et al., 2016), probably because it represents the simplest way to measure biodiversity (Colwell and Coddington, 1994). Nevertheless, it presents relevant shortcomings. Firstly, species richness is highly prone to scale issues, which may result in misleading conclusions for conservation (Gotelli and Colwell, 2001; Chiarucci et al., 2011). In fact, fine-scale partitioning of resources may generate patterns of species diversity not properly addressed if focusing only on one fixed spatial scale (e.g., Standovár et al., 2006). Further, high species richness within stands (i.e., alpha-diversity) may mask lower levels of diversity across stands (i.e., beta diversity) with homogenization at regional level (i.e., gamma-diversity) (Schall et al., 2018). Secondly, species richness may be misleading if adopted as an indicator for the conservation status of the forests. For instance, Boch et al. (2013) suggested species richness of vascular plants as indicator for disturbance by management. Indeed, plants may benefit from resource increase (such as light or nutrients) following moderate disturbance by management or other human uses (Roberts, 2004; Christensen and Heilmann-Clausen, 2009).

To account for these shortcomings, many researchers have focused on subsets of **conservation-relevant species** (Dolman et al., 2012). Red-listed species have been used to assess the conservation value of forests (Flensted et al., 2016), while other studies have focused on species with specific habitat requirements and/or particular biological attributes. For example, cavity-nesting birds have been adopted as target species to indicate critical thresholds of veteran trees and microhabitat abundance (Winter and Möller, 2008). These target species are often associated with old-growth forests conditions, including stand continuity (Hermy and Honnay, 1999; Schmidt et al., 2014). In many cases, however, the links between species and habitat conditions remain poorly understood or the bioindication is so obviously circular that the indicators have little relevance (Nordén et al., 2014; Halme et al., 2017).

Recently, **functional approaches** have been proposed as an alternative way to assess the impact of forest management on biodiversity (e.g., Giordani et al., 2012; Aubin et al., 2013). By focusing on the “kinds” of species rather than their numbers, a functional approach potentially gives a better understanding of the mechanisms driving habitat changes and species assemblages (Pausas and Verdú, 2010), allowing also comparisons across different ecosystems, regions and management systems. This approach may therefore be suitable to capture ecosystem properties and the effects of disturbances (e.g., Bässler et al., 2016a, 2016b). Despite these potentials, the reliability of functional measures is still not well known.

In all, choosing one metric of biodiversity over another may have substantial consequences on the evaluation of conservation tools. However, the consistency of different metrics is still scarcely investigated, especially in a multi-taxon framework, limiting applicability in practice.

The aim of our study was to investigate if different metrics of diversity show consistent patterns along a management-related environmental gradient, from long unmanaged to even-aged managed stands of European beech. We investigated how different diversity metrics (i.e., total species richness, richness of conservation-relevant species, and functional diversity) were related to this gradient, and hence may be indicative for the variation of forest attributes (i.e., structural and environmental ones) across five organism groups (vascular plants, epiphytic lichens and bryophytes, saproxylic fungi and birds).

We expected a non-consistency among the compared metrics, as well as among organism groups. Concerning the (1) **total species richness** (at stand level), we expected vascular plants to be favoured by human disturbance, in contrast to the other organism groups, but with a weak response of birds more likely depending on habitat suitability on a higher spatial scale than the stand level. Nevertheless, accounting only for the (2) **richness of conservation-relevant species** we hypothesised a general decrease from the long-unmanaged to the managed stands. Consistent with

this trend we expected a homogenization of (3) **functional diversity** (at single-trait level) for all the organism groups, with a trend towards more generalist strategies, broad ecological niches and higher dispersal ability as response of disturbance by management.

2 Materials and methods

2.1 Study area

The study was conducted in Gribskov, one of the largest coherent forests in Denmark, covering an area of almost 6.000 ha (*Figure 1*). The terrain is undulating (9-89 m a.s.l.), with numerous boggy depressions. The topsoils are generally developed as mor or moder on glacial sandy to gravelly deposits stemming from the Weichelian glaciation. The forests are shaped by two centuries of timber oriented forestry, with European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) H. Karst.) dominating and largely found as even-aged monocultures. European beech established in the area almost 6000 yrs ago, but became dominant only within the last 1000 yrs (Overballe-Petersen et al., 2013), while Norway spruce was introduced with modern forestry during the latest 250 yrs (Rune, 2009). Only small remnants of old-growth forests are left, mainly as stands smaller than 5 ha. The climate is temperate with an average annual precipitation of 697 mm and an annual mean temperature of 7.7° C.

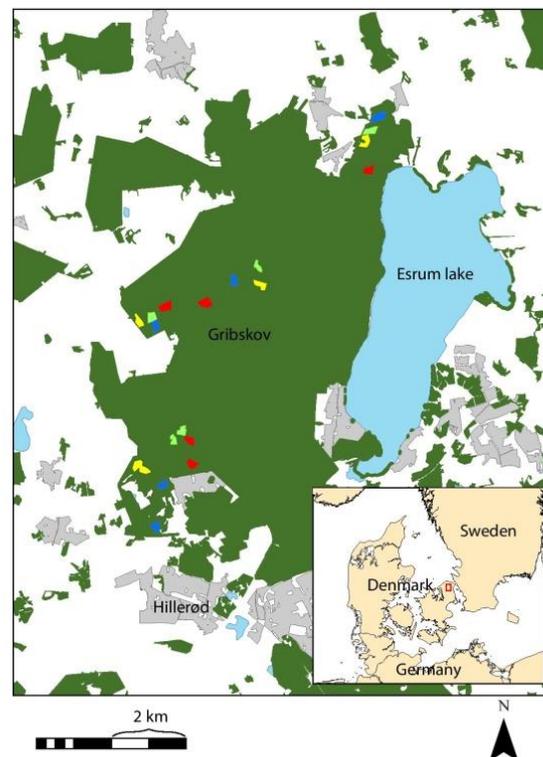


Figure 1 Study area (Gribskov, Denmark). The forest stands along the gradient of management intensity are shown with different colours (blue = long-unmanaged, yellow = recently unmanaged, red = managed, light green = nat. managed). In dark green the forest system including all the stands.

2.2 Data collection

Twenty forest stands, each 3 ha in size, were selected based on existing information and field visits during winter/spring 2015, using a stratified random sampling design to secure a balanced representation of management impact over space and time in the study landscape. The stands were selected to represent four broad classes based on management history and structural attributes in five replicates. Each class was defined based on detailed information in Graae and Buchwald (1997): 1) stands unmanaged for more than 50 years with dominant trees older than 200 years; 2) stands unmanaged for less than 50 years with dominant trees older than 100 years; 3) extensively managed biodiversity stands with dominant trees older than 100 years, and components of structural heterogeneity, in the form of a multi-layered canopy and the presence of at least some coarse woody debris (CWD); and 4) intensively managed stands with dominant trees older than 100 years, a simple structure with one or two dominant tree layers and no or little CWD. All selected stands were dominated by European beech (> 60 % of basal area). Due to the rarity of long-unmanaged stands, these were selected first. In the second step, the topography, geography and general growth conditions (soil type) of the long unmanaged stands were used to guide the selection of stands in the other management categories, which were aggregated in four clusters containing one or two replicates of each management type (*Figure 1*). To account for random and non-random spatial effects, we selected forest stands occurring in clusters where each of the four management levels is represented.

To sample the stands and collect species data, we randomly placed ten 50 m transects and ten circular plots with 5 m radius, respecting a minimum distance of 30 m between the plots. Up to five of the random plots were subsequently substituted with an equal number of plots strategically placed so as to best capture vegetation variations within each stand. Vascular plants were sampled on plots, while saproxylic fungi were sampled on transects. Epiphytes were investigated on ten trees within each stand, selected to maximize the occurrence of species of conservation concern. In each stand we identified potential host trees for epiphytes of conservation concern, i.e., focussing on old slow-growing or damaged trees in contrast to healthy well growing trees (e.g., Fritz, 2009; Fritz, 2011). Saproxylic macrofungi (including polypores, agarics, pileate corticioids, thick resupinate corticioids, i.e., species from the genera *Coniophora*, *Phlebia* and *Steccherinum*, larger discomycetes and stromatic pyrenomycetes) were recorded on all sampled dead wood during two separate field visits (late Aug/early Sept and late Oct). At the latter sampling date, a stand-level survey (maximum 1 hr per stand) was conducted to record supplementary species. A quantitative estimate of breeding birds was acquired by territory-mapping (Bibby et al., 2000). The surveys were scheduled to span the breeding season of all potential breeding birds: end of April to end of June.

The sites were visited in the early hours of the day, until around noon, where song activity is most intense. Days of rain and strong wind were generally avoided. Each study site was surveyed a total of 9 times. Each visit lasted around 45 minutes, depending on bird activity and local conditions, and entailed both visual and auditory observations. On the basis of the completed set of field maps, final species maps were produced, quantifying the number of breeding bird territories for all observed species. Territories that extended beyond the boundary of any given stand were counted as halves (Bibby et al., 2000).

The mapping of forest development phases was based on Emborg et al. (2000) with three amendments. First, the limit between early and late biostatic phase was set to a tree diameter of 70 cm DBH. Second, the degradation phase was expanded to embrace all situations where canopy cover was missing without regeneration being established. This included canopy gaps from tree felling in the shelterwood phase in managed stands, as well as natural canopy gaps with high grazing pressure and grassy vegetation. Third, wetlands with sufficiently high water table to hamper tree growth were mapped separately as wetlands.

Tree microhabitats were recorded based on a protocol modified from Winter and Möller (2008), differentiating ten main tree microhabitat types: a) broken crown, b) bark missing on trunk > 400 cm², c) bark loose on trunk > 400 cm², d) trunk cavities with entrance > 5 cm in diam., e) trunk cavities with entrance < 5 cm in diam., f) pockets aggregating stagnant water or mould, g) fruit bodies of saproxylic fungi, h) cankers, i) wood-pecker holes and j) sap flow. The survey method adopted for each variable is summarized in *Table 1*.

Table 1 Description and survey methods for the structural variables used in the PCA ordination and for the organism groups. Levels: Stand (S); Plot (P); Transect (T); Ten European beech trees in each stand (Tr).

Structural variable	Description	Level	Survey/Source
AGE	2015 minus the establishment year of the (dominant trees of the) forest stand	S	State forest data from forestry maps
IS	Innovation stage, with openings and presence of tree regeneration (saplings)	S	Mapped following Emborg et al. (2000).
DS	Degradation stage, with presence of gaps, undergrowth (herbs and shrubs) but still not tree regeneration	S	Mapped following Emborg et al. (2000) with amendments (see main text).
W	Presence of wetland sites too wet to sustain tree growth	S	
MHT	Presence of microhabitats on trees with a DBH > 80 cm (veteran trees)	T	Mapped in a 10 m band along each transect
T	Topography: range between the upper and the lower elevation (meters a.s.l.)	S	Extracted from GIS analysis of topographic maps
pH	Average soil pH values	P	Based on four replicate soil samples (excluding litter) in each plot down to a depth of 10 cm
pHR	Range of soil pH values	P	As above
CWDF	Amount of fallen coarse woody debris (diam. > 10 cm.)	T	Sampled along each transect following Bate et al. (2009).
FWD	Amount of fine woody debris (diam. 5-10 cm)	T	Sampled along the first 10 m of each transect following Bate et al. (2009).
CWDS	Amount of standing coarse woody debris (diam. > 10 cm.)	T	Measured in a 10 m band along each transect
STUMPS	total number of cut stumps	T	
BA	Tree basal area (volume) - Living trees with DBH > 10 cm	T	
Organism groups	Description	Level	Survey/Source
Vascular plants	Vascular plants of the forest floor: herbs, shrubs, seedling and saplings of trees < 2 m tall	P	Presence/absence within each plot
Epiphytes	Lichens and bryophytes	Tr	Presence/absence from the base of the trunk up to 2 m height.
Saproxyllic fungi	Fruit bodies of saproxyllic macrofungi	T	Presence/absence on each recorded dead wood item
Birds	Breeding pairs	S	Presence/absence per stand

2.3 Functional traits

Firstly, to investigate changes in functional diversity of each organism group as a response to management and other stand variables, we selected traits used in previous studies of forest biodiversity. To standardize as much as possible trait selection across groups, we considered how individual or species performance at a given site is determined by three main characteristics: acquisition, preservation and dispersion of resources over time (Garnier et al., 2016).

Therefore, we first selected traits related to acquisition and preservation of resources and providing information about the structure of the assemblages. For vascular plants, we included the woodiness (Kleyer et al., 2008), which is informative of variations in the structural heterogeneity of assemblages. We classified epiphytic lichens by algal partner (photobiont type) and growth-forms (Nimis and Martellos, 2017), as they are both related to assemblage structure and response to disturbance and forest structural changes (Giordani et al., 2012; Nascimbene and Marini, 2015).

Bryophytes were classified into growth-forms (During, 1992), which depend on abiotic environmental conditions, notably water resources and substrate affiliation (During, 1979, 1992). For fungi we included traits responsive to habitat changes (Nordén et al., 2013; Bässler et al., 2016b), related to fruit body size and type, and tree host preference (mainly based on Knudsen and Vesterholt, 2012 and Ryvarden et al., 2014). Birds were classified according to body mass (Gotelli et al., 2010), dietary specialization ([DOF](#), 2018), and nesting site (Svensson et al., 2010) and response to structural and environmental changes (Newbold et al., 2012).

Secondly, we compiled traits related to the dispersal potential within each organism group: reproductive strategy (Fitter and Peat, 1994) and dissemination vectors (Julve, 1998) for vascular plants (Graae and Sunde, 2000), main reproductive strategies (Nimis and Martellos, 2017) for lichens (e.g., Ellis, 2012; Giordani et al., 2012; Nascimbene et al., 2017), and dispersal vectors for saproxylic fungi responsive to forest structure and fragmentation (Heilmann-Clausen et al., 2014; Bässler et al., 2016b).

Thirdly, as an attribute of ecological performance (Violle et al., 2007) we included Ellenberg indicator values for light (EIV, Ellenberg, 1974), available for vascular plants, lichens, bryophytes and fungi (Ellenberg et al., 1991; Hill et al., 2007; Wirth, 2010; Simmel et al., 2017). Indeed, light availability is an abiotic resource strongly influenced by forestry operations.

Finally, as organisms' responses to environmental variability always involve a combination of traits, we included a classification of ecological strategies (Garnier et al. 2016) for plants and bryophytes. Life-strategies for plants were drawn from Klotz et al. (2002) following Grime (2001). This three-strategy model (CSR) is based on a set of traits matching different combinations of habitat favourability and disturbance. A life-strategies classification for bryophytes was proposed by During (1979) based upon traits that often occur together and indicate disturbance tolerance (plants endure the stress period with their vegetative part) or avoidance (plants disappear leaving stress-tolerant diaspores). All traits and attributes selected are listed in *Table 2*.

Table 2 Description of the functional traits and attribute of ecological performance selected from the available literature and analysed in this study. Data types: continuous (quantitative) and categorical (binary, nominal, ordinal).

Taxa	Trait	Data type	Range/Categories
Vascular plants	Woodiness	Binary	Woody, Non-woody
	Light indication	Ordinal	1 - 9
	Reproductive strategy	Nominal	Seeds and vegetative, Seeds
	Dissemination vector	Nominal	Anemochory, Dyszoochory, Endozoochory, Epizoochory, Myrmecochory, Autochory, Barochory, Hydrochory
	Life-strategy	Nominal (fuzzy)	Competitors, Stress-tolerators, Ruderals
Lichens	Growth-forms	Nominal	Crustose, Foliose narrow-lobed, Foliose broad-lobed, Fruticose
	Photobiont type	Binary	Chlorococcoid algae, Trentepohlia
	Light indication	Ordinal	1 - 9
	Reproductive strategy	Nominal	Sexual reproduction, Sorediate species, Isidiate species
Bryophytes	Growth-forms	Nominal	Cushions, Mats, Turfs, Others (Wefts, Tails, Dendroids: types with less than 5 species)
	Light indication	Ordinal	1 - 9
	Substrate	Nominal	Epiphytic, Opportunistic, Terricolous
	Life-strategies	Nominal	Colonist, Long-lived shuttle, Perennial
Fungi	Fruit body size*	Quantitative	0 - 1
	Fruit volume (Agaric)		20.5 mm ³ - 244756.5 mm ³
	Fruit thickness (Polypores)		1.5 mm - 250 mm
	Fruit body type	Nominal	Agaric, Crustose, Polypore, Stroma, Others (types with less than 10 species)
	Light indication	Ordinal	1 - 9
	Host preference	Nominal	Both (coniferous/deciduous), Coniferous, Deciduous, European beech (<i>Fagus sylvatica</i> L.)
	Dispersal vectors	Binary	Asexual spores, Mycelial cords
Birds	Body mass	Quantitative	5.8 g - 1200.5 g
	Summer foraging guilds	Nominal	Omnivore, Herbivore (seeds and herbs), Insectivore, Prey
	Nesting site	Nominal	Undergrowth, Trees, Tree hollows

* Fruit body size: normalized values of volume and thickness for the Agaric and Polypore types, respectively.

2.4 Data analysis

All analyses were conducted using stand level data, aggregated across sample trees (epiphytes), plots (vascular plants, soil pH, light conditions), transects (saproxylic fungi, variables related to living trees and dead wood), or the whole stand (birds, forest development phases, wetland areas). Our approach was to focus on the measured structural and environmental variables, rather than the four a priori defined management classes used in the selection of study sites. This choice was based on the observation that intermediate structural/environmental situations characterized many of the surveyed stands, which were thus better represented along gradients than as distinct categories. Following the approach of previous studies (e.g., Bässler et al., 2016a) we applied principle component analysis (PCA) on the set of environmental and structural variables of each stand in order to reduce dimensionality of the complex conditions characterizing the study sites. We then used the scores of the first two PCA axes (henceforth, PC1 and PC2) as input variables to investigate biotic responses to changes in forest structure and environmental factors. We did not model the response of individual diversities to individual structural/environmental variables since our goal was to compare the response of the different organism groups (and sub-groups within

these), using the three diversity metrics, to common structural/environmental gradients. This approach also resulted in higher statistical power, since we could describe our environmental space using only two gradients. As an alternative to the PCA based classification we considered the option to use pre-defined indexes to define the level of management impact (e.g., Gossner et al., 2014; Kahl and Bauhus, 2014), but this approach was disfavored due to the embedded subjective decisions involved in weighing the different primary metrics on which these are calculated.

We ran generalized linear mixed model GLMMs (Bolker et al., 2009) with the scores of PC1 and PC2 as fixed effects and with the four spatial clusters of forest stands as random effect. As response variables we used in turn: (i) species richness, (ii) richness of conservation-relevant species, and (iii) functional diversity for each organism group. The models assumed (a) a Poisson distribution of errors for count data, (b) a Gaussian distribution of errors for continuous data, and (c) a Binomial distribution of errors for binary data and for frequencies.

(i) **Total species richness** was measured by counting the number of species occurring in each stand. The richness of (ii) **conservation-relevant species** was calculated in the same way, considering a subset of species included in the Danish Red-Lists (RL) (Wind and Pihl, 2004) and in lists of old-growth indicators species, mostly considered associated with long temporal forest continuity (Nordén et al., 2013), based on Hermy and Honnay (1999) and Schmidt et al. (2014) for vascular plants, and Hallingbäck and Aronsson (1998), Thor and Arvidsson (1999), Nitare (2000) and Christensen et al. (2005) for bryophytes, lichens and wood-inhabiting fungi. The supplementary species of saproxylic fungi were included in these counts.

(iii) **Functional diversity** was analysed by computing the community-weighted mean (CWM) and Rao's quadratic entropy coefficient (RaoQ) at the single-trait level, weighted by the frequency of each species at stand level (Ricotta and Moretti, 2011; Curzon et al., 2017). To measure the frequency, we counted in how many sampling units (plots/transects/trees at stand level) each species was present. With the CWM, we measured shifts in mean trait values for each trait, expressing the central tendency for quantitative traits and the relative frequency of a given trait in a species assemblage for ordinal and nominal data (binary and dummy/fuzzy traits) (Garnier et al., 2004; Ricotta and Moretti, 2011). With the RaoQ index, we analysed patterns of trait convergence or divergence (i.e., a decrease or increase in trait dissimilarity compared to a random expectation) (Mason et al., 2005; Lepš et al., 2006).

To compute CWM and RaoQ, we coded as ranks the ordinal data (e.g., EIV), while we expanded the nominal traits into binary data (e.g., woody/not woody) or dummy variables if more than two categories were present (e.g., growth-forms). Nominal traits including categories with intermediate possibilities were coded as fuzzy variables (e.g., life-forms) (*Table 2*).

All analyses were performed using R statistical software version 3.4.2 (R Core Team, 2017) with the packages “ade4” (Dray and Dufour, 2007), “factoextra” (Kassambara and Mundt, 2016), “lme4” (Bates et al., 2015) and “FD” (Laliberté et al., 2015). The “FD” package was used to calculate RaoQ and CWM with the function dbFD() for ordinal, binary and quantitative data while the function functcomp() was used for nominal data coded as dummy or fuzzy variables. Functional traits for the vascular plants were retrieved from the “TR8” package (Bocci, 2015).

3 Results

The first principal component (PC1) of a PCA based on forest structural attributes accounted for 33.5% of the explained variation in the range of environmental predictors (*Table 1*) and captured a gradient in management-related environmental variables, with long-unmanaged stands clearly differentiated from stands in the three other stand classes (*Figure 2*).

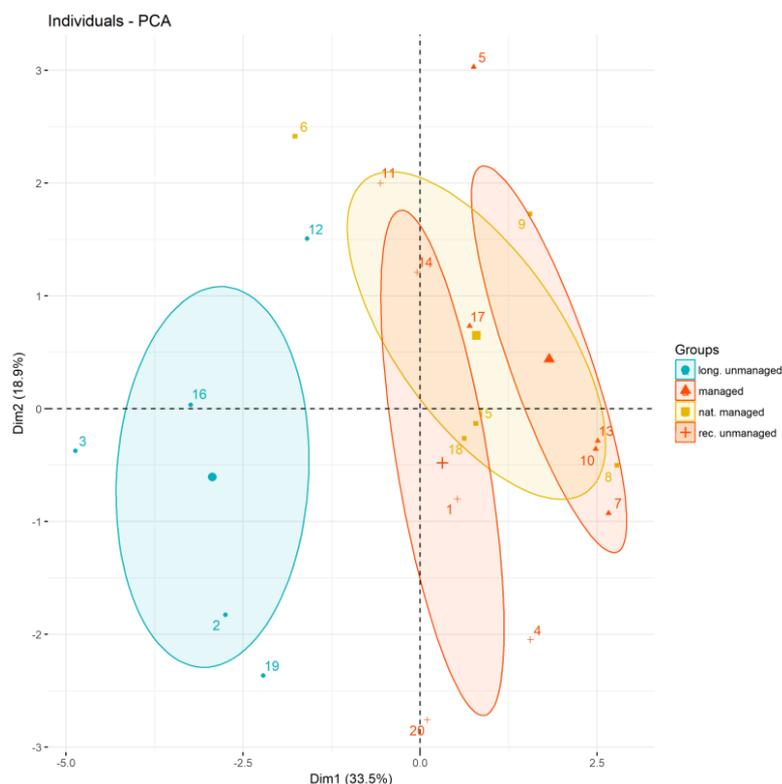


Figure 2 PCA ordination performed on the structural variables at stand level listed in Table 1, with groups indicating the coarse management classes: long-unmanaged (for more than 50 years), recently unmanaged (for more than 30 years), naturally managed (structurally complex, with presence of dead wood), and managed (structurally simple). The first component (PC1) mainly expresses the levels of management characterized by structural differences among the four classes (from long-unmanaged stands to managed ones). This is supported by an ANOVA test followed by a posthoc Tukey test showing that the scores of PC1 are significantly different among the management classes, with especially a strong differentiation of the long unmanaged stands compared to the others.

Presence of veteran trees and high basal area differentiated long-unmanaged stands with low axis scores from intensively managed stands with high amounts of stumps and high axis scores (*Figure 3*). The second component (PC2) accounted for 18.9% of the explained variance and was mostly

related to topography, canopy openness and soil productivity. Low axis scores were associated with high soil pH and presence of wetlands, while hilly topography and high light availability (forest openings) characterized stands with high axis scores (*Figure 3*). The amount of coarse woody debris and stand age were correlated with both PC1 and PC2, with highest values in unmanaged stands on less rugged and more productive soils. The wide scatter of short unmanaged and extensively managed stands in the ordination space reflects that these are highly heterogeneous, reflecting differences in historical management.

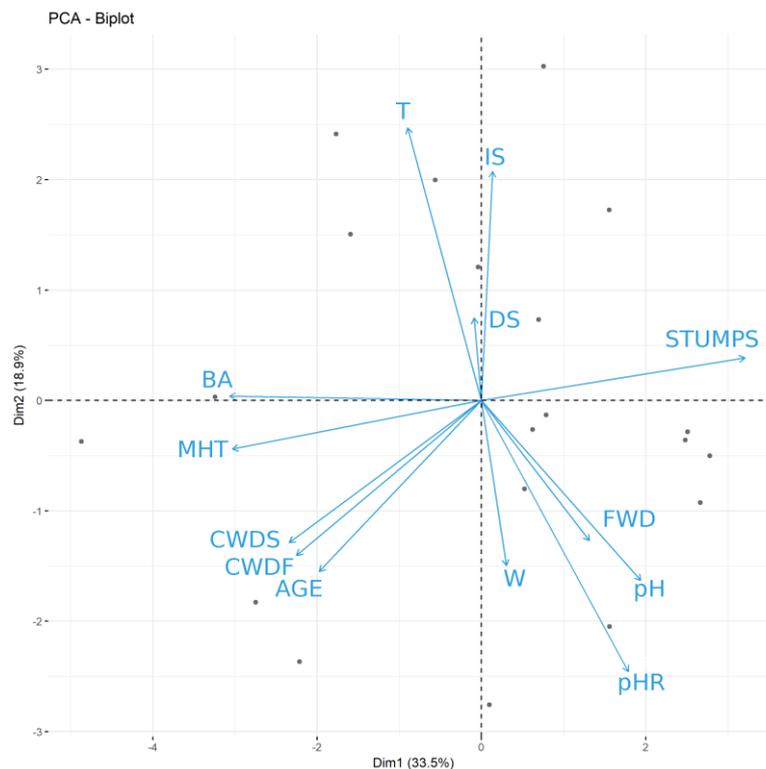


Figure 3 PCA ordination performed on the structural variables at stand level in Table 1. The first axis (PC1) accounts for 33.5% of the explained variation in the range of environmental predictors, mainly expressing changes in management-related environmental variables from long-unmanaged to managed stands: the presence of veteran trees (MHT) and a high basal area (BA) differentiated long-unmanaged stands with low axis scores, while in the opposite direction high amounts of stumps characterize the most intensively managed stands. The second axis (PCA2) accounts for 18.9% of the explained variance and represents a main gradient of site productivity/canopy openness across stands unrelated to management (an ANOVA test performed on the scores of PC2 vs the management classes indicates no significant differences among the classes). This gradient is mostly related to topography (T) (+), canopy openness (IS, DS) (+) and soil productivity (-): low axis scores are associated with high soil pH (pH, pHR) and presence of wetlands (W), while hilly topography and high light availability (forest openings represented by the innovation and the degradation stages, IS, DS) characterized stands with high axis scores. The amount of dead wood (CWDS, CWDF) and stand age is correlated with both PC1 and 2, showing highest values in unmanaged stands on flatter and more productive soils.

A total number of 130 vascular plant species (mean = 36.8, SD = 9.3 at stand-level), 78 species of epiphytic lichens (mean = 29.6, SD = 8.2), 29 species of epiphytic bryophytes (mean = 9.8, SD = 2.6), 209 species of saproxylic-fungi (mean = 54.4, SD = 11.2), and 33 species of birds (mean = 16, SD = 2.6) were recorded in the 20 stands. For 162 species of saproxylic fungi we calculated frequency data at stand level, since they were recorded along the ten transects of each

stand. Only these species were included in the analyses of functional diversity. The remnant 47 species (supplementary species) were recorded in the last stand-level survey, with only presence/absence annotation at stand level.

The (i) stand-level **species richness** of vascular plants was positively correlated to PC1, while this relation was negative in the case of saproxylic fungi and epiphytic lichens. Similarly, stand-level richness of epiphytic lichens was positively associated with PC2, while saproxylic fungi showed a significant negative relation with the same gradient (*Table 3*).

Concerning the (ii) **conservation-relevant species**, red-listed species were only recorded among lichens (42) and wood-inhabiting fungi (15), and were negatively related to changes in management-related environmental variables expressed by PC1 (*Table 3*). Fungi were negatively related also to the forest structural gradient expressed by PC2, while the relation of red-listed species of lichens to this gradient was marginally positive (*Table 3*). The old-growth indicator species of lichens (12 species), bryophytes (7), and saproxylic fungi (29 species) decreased with PC1 (*Table 3*), while vascular plant indicator species (32 species) showed a positive trend along the same gradient, using both lists in Hermy and Honnay (1999) and Schmidt et al. (2014). Negative relations with PC2 were found for vascular plants and saproxylic fungi (*Table 3*).

Table 3 Results of GLMMs using species richness (SR), conservation relevant species (red-listed species RL and old-growth forest specialists OG) as response variables and scores of the first two PCA-axes as fixed effects (random effect: spatial clusters of stands). PCA ordination was performed on the structural variables in Table 1.

+ and – symbols denote positive or negative trend, respectively
 ns, not significant, ° p-value < 0.1, * p-value < 0.05, ** p-values < 0.01
 a, none of the sampled species listed as RL or OG

Organism group	PC1			PC2		
	SR	RL	OG	SR	RL	OG
<i>Vascular plants</i>	+***	a	+*	ns	a	-°
<i>Lichens</i>	_*	_-***	_-***	+*	+°	ns
<i>Bryophytes</i>	ns	a	_-***	ns	a	ns
<i>Fungi</i>	_*	_-**	_*	_-***	_*	_-***
<i>Birds</i>	ns	a	a	ns	a	a

A relation of (iii) **functional diversity**, measured as functional divergence (RaoQ) and CWM, with PC1 was found to be significant especially for vascular plants (*Table 4, Figure 3*), as the relative occurrence and functional divergence of woody species decreased from long-unmanaged to managed stands along PC1. We also found an increasing similarity in reproductive strategies (i.e., increasing proportion of generalist species with both vegetative and sexual reproduction) and dissemination vectors, with an increasing occurrence of epizoochorous species, at higher axis values. Stress-tolerators showed a near-significant positive relation with the gradient, as opposed to competitive species. Among the other organism groups, cushion-shaped epiphytic bryophytes had a positive relation with PC1, while there was a decrease of other growth-forms (including wefts, tails,

and dendroids). Species with higher EIV increased along PC1, together with an increasing trait-divergence. Saprophytic fungi with a generalist preference for deciduous wood showed a positive relation with PC1, contrary to species with a species-specific host preference for European beech (*Fagus sylvatica* L.).

Along the second axis (PC2, Table 4) we found an increasing occurrence of vascular plants with high EIV. Functional divergence in lichens growth-forms also rose along PC2, accompanied by higher occurrence of foliose broad-lobed species versus crustose species. The occurrence of lichens with an asexual reproduction was also positively related with PC2, while species with a sexual reproduction decreased. Regarding the bryophytes, the number of mat-shape species declined along PC2, while turfs increased. Saprophytic fungi showed the same trend as described for PC1, with an increase in generalist substrate requirements and a decrease of host-specialists.

Table 4 Results of GLMMs using single-traits/attributes as response variables and scores of the first two PCA-axes as fixed effects (random effect: spatial clusters of stands). PCA ordination was performed on the structural variables in Table 1. Only traits with significance relations are reported. RaoQ: Rao index of functional divergence; CWM: community-weighted mean for quantitative traits and relative proportion of a given trait in the species assemblage for the nominal (dummy/fuzzy) and binary data.

+ and – symbols denote positive or negative trend, respectively;
ns, not significant, ° p-value < 0.1, * p-value < 0.05, ** p-values < 0.01

Organism group	Traits/Attributes	PC1		PC2	
		RaoQ	CWM	RaoQ	CWM
<i>Vascular plants</i>	Woodiness	–**	–***	ns	ns
	Light intensity	ns	ns	ns	+**
	Reproductive strategy	–**		ns	
	Seeds and vegetative		+***		ns
	Seeds		–***		ns
	Dissemination vector	–**		ns	
	Anemochores		–***		ns
	Epizoochores		+***		ns
	Life-strategy	ns		ns	
	Competitors		–*		ns
	Stress-tolerators		+°		ns
<i>Lichens</i>	Growth-forms	ns		+*	
	Foliose broad-lobed		+°		+**
	Crustose		–°		–**
	Reproductive strategy	ns		+°	
	Isidiate species		+°		+**
	Sorediate species		ns		+*
	Sexual reproduction		ns		–***
<i>Bryophytes</i>	Growth-forms	ns		ns	
	Cushions		+***		ns
	Mats		ns		–*
	Turfs		ns		+*
	Others		–***		ns
	Light intensity	+*	+**	ns	ns
	Fungi	–**		–**	
Host preference					
Deciduous		+***		+**	
European beech		–***		–***	
Dispersal vectors	ns		+°		

4 Discussion

We found that simple species richness, versus a trait/"indicator" based approach showed inconsistent patterns along the structural and environmental gradients investigated in European beech forests.

The main findings are that (i) the measure of stand-level species richness obscured changes in the number of (ii) conservation-relevant species (old-growth specialists and red-listed species). The (iii) functional approach mostly captured variations in vascular plant assemblages from long-unmanaged to intensively managed stands, while signals were less clear with regards to the other organism groups. Species richness of vascular plants (including old-growth specialists) increased from long-unmanaged to managed stands along PC1, showing an opposite trend compared to the other organism groups. However, the functional approach indicated that this increase was mainly due to establishment of species with generalist traits, in particular high dispersal potential and affiliation with disturbed habitats in general.

4.1 Species richness

Stand-level species richness was weakly sensitive to changes in forest structure from long-unmanaged to intensively managed stands, but with lack of congruent patterns across different organism groups, as also reported in other studies (e.g., Christensen and Heilmann-Clausen, 2009; Paillet et al. 2010, Sitzia et al., 2017). In fact, only the richness of vascular plants showed an increase with changes in management-related environmental variables from long-unmanaged to managed stands, in contrast to the number of conservation-relevant species of wood-inhabiting fungi, epiphytic lichens and bryophytes. This strongly supports that species richness of vascular plants is poorly suited as a proxy indicator of conservation value for other groups of forest organisms, as also reported by Sabatini et al., 2016. Our results even question the relevance of stand level species richness among the other groups considered. Focusing on total species richness, without considering the number of conservation-relevant species, may lead to misleading conclusions for conservation purposes due to a non-consistency among the two metrics. For instance, we found that a non-significant variation in the species richness measured for the epiphytic bryophytes did not reflect a significant decrease of conservation-relevant species at changing management-related environmental variables.

Therefore, we argue that the richness of conservation-relevant species can be suited as indicator of management impact, but only for some organism groups (i.e., epiphytes and saproxylic fungi in our study) and in a well described context. According to the approach adopted in this study, we refer to management impact considering changes in management-related environmental variables (e.g.,

reduction in the presence of veteran trees and basal area and increase in the amount of stumps from long-unmanaged stands to intensively managed stands). The higher number of conservation-relevant species of saproxylic and epixylic organisms (fungi and epiphytes) found in the long-unmanaged stands can be interpreted as a signal of (i) recovery of favourable habitat conditions, reflecting the time since abandonment of forestry (Burrascano et al., 2008), or as an effect of (ii) higher continuity, with the persistence of suitable legacy habitats for sensitive or slow dispersing species, in stands less affected by forestry. Among the epiphytes for instance, many substrate specialists require the persistence of old beech trees because suitable microhabitats, such as rough bark and rot holes, only develop at high tree age, often on slow-growing and suppressed trees (Fritz and Brunet, 2010).

Nevertheless, we found a contrasting pattern for the vascular plants. We were somewhat surprised to measure higher richness of vascular plants listed as old-growth indicators (*sensu* Hermy and Honnay, 1999; Schmidt et al., 2014) in the managed stands, but similar patterns were found also by Boch et al. (2013), who studied vascular plants in 1500 plots in European beech forests, comprising several management types and stand ages. They found a higher richness of typical herbaceous forest species in the managed compared to unmanaged stands, likely favoured by higher availability and heterogeneity of resources (such as light, nutrients) with moderate disturbance by management. Thus, environmental conditions in production forests may not be unfavourable for plants identified as old-growth indicators. In this context it is worth emphasizing that the old-growth indicator plants were identified based on studies comparing managed forests with various continuity levels, but with generally low naturalness in European lowlands. Hence, they may indeed be very suitable for identifying forest characterized by high forest connectivity and continuity, as for our study area, but not forests with low impact of forestry. In contrast, old-growth indicators of lichens, bryophytes and fungi have generally been selected to indicate forests with low management impact (e.g., Nitare, 2000; Christensen et al., 2005), and hence were expected to be more responsive to changes in management-related environmental variables. However, studies of biodiversity responses to forest management intensity in Europe need also to acknowledge that the whole system is strongly human-modified, even in the case of long-unmanaged stands or remnant old-growth forests. In such systems, extinction debts and credits may create odd biodiversity patterns, deviating from patterns in forest systems subject to more recent degradation and management. Furthermore, because most of the unmanaged forests were formerly managed to some degree, they probably have not yet reached natural levels of habitat variation (e.g. concerning dead wood and veteran trees) (Sabatini et al., 2018). More generally, structure, processes and natural disturbance events which may increase habitat heterogeneity and the resource availability for several species groups in old-growth forests,

may still be not evident even in many long-unmanaged forests (Burrascano et al., 2017; Schall et al. 2018).

Another important issue is **spatial scale**. Drivers of forest biodiversity may act at different spatial scales depending on forest maturity, management regime and the organism group considered, leading to very different richness patterns at different scales (e.g., Standovár et al., 2006; Burrascano et al. 2018). Recently, Schall et al. (2018) showed how differently grained forest management systems affect the biodiversity of multiple taxa across spatial scales, finding that a mosaic of different age-classes is more important for regional biodiversity than high within-stand heterogeneity. In fact, they measured higher regional gamma-diversity in even-aged forests compared to uneven-aged forests driven by between-stand beta diversity and not by local alpha-diversity. This indicates that only focusing on stand-level species richness (alpha-diversity) may mask patterns of diversity occurring at different spatial scales. In this context it is worth emphasizing that our sampling of epiphytes and vascular plants was optimized to capture stand-level species richness as well as possible, rather than to follow a random protocol or a full inventory as implemented for fungi and breeding birds. While this was done to control for the highly patchy nature of plant communities in natural forests (cf. Kaufmann et al., 2017), and of conservation-relevant epiphytes in managed forests (Fritz, 2009), this may boost the measured species richness in our studies, compared to those using a completely random sampling.

Although our study was mainly focused on the responses to changes in management-related environmental variables along PC1, some of the species richness responses to structural factors expressed by PC2 are also worth discussing. For instance, the positive response of lichen species richness, including red-listed species, suggests that this group can be favoured by the heterogeneous conditions in canopy cover generated through stand clearings, as also found in previous studies (e.g., Giordani et al., 2012; Ódor et al., 2014). Finally, the negative trend of fungal richness along PC2 is most likely related to higher productivity and the resulting higher dead wood amounts in the denser stands on flat ground with less acidic soils. We hypothesize that the habitat suitability (i.e., presence of available substrate) is probably the main driver which promotes richer wood-inhabiting fungi assemblages in our study system. However, other interrelated factors, like soil and wood moisture and pH, may also play a role in regulating the activity and richness of wood decaying organisms (cf. Pouska et al., 2016; Bardelli et al., 2018).

4.2 Functional diversity

The functional approach partly confirmed the expectation that functional diversity decreases with changes in management-related environmental variables from long-unmanaged to managed stands,

but the results were complex. The clearest results were found for assemblages of vascular plants with a higher occurrence of herb species (e.g., Šebesta et al., 2017) and species with generalist dispersal strategies from long-unmanaged to managed stands. For the other groups, responses were more varied, but consistent with a loss of specialization and progressive banalization of species assemblages. We measured a decline in resource specialists wood-inhabiting fungi (i.e., specialized saproxylic fungi confined to European beech wood) likely linked to a decrease in substrate availability (Nordén et al., 2013). Similarly, the predominance of bryophytes with higher light requirements and cushion-shape growth has earlier been linked with disturbance and with a reduction in habitat continuity (such as canopy cover) (During, 1979; Brunet et al., 2010).

However, the loss of specialization and the increase in more generalist strategies do not necessarily imply a reduction in functional diversity. Indeed, previous studies found that disturbance events even due to forestry activities may promote more diverse species assemblages. For instance, a partially or completely removed forest canopy (as a result of natural disturbance or management) compared with undisturbed forest patches, was found to promote the diversity of several functional groups, including pollinators and arthropod herbivores, likely driven by increased diversity and abundance of plants (Campbell and Donato, 2014). In our study, gaps in the canopy cover favoured especially light-demanding herb species, as well as lichens with vegetative reproduction strategies and more diverse growth-forms (Ellis, 2012).

As also demonstrated by the examples above, the functional approach may effectively complement effective diversity surveys (Blüthgen et al., 2016). In fact, species assemblages may change functionally without significant changes in species richness or in the number of conservation-relevant species. In our study, this was the case for bryophytes, for which the change in the dominance of growth-forms was not reflected in a variation of species richness. Finally, the generally weak functional response of birds may reflect their dependence on forest conditions at a wider landscape scale (Aubin et al., 2013) than at stand level, especially in contexts of high forest continuity and connectivity. Stronger changes of animal communities have been evidenced especially with more marked habitat changes, like the conversion of forests into open grasslands, than for gradual variation of forest structure and management (Blüthgen et al., 2016).

Overall, the clearest functional signal related to forest management and structure was found for vascular plants. This may reflect that this group is better understood and described in terms of functional traits (Cornelissen et al., 2003), while trait-based approaches remain less developed for the other organism groups considered. However, despite the informative potential of the functional approach, at present the limited number of measured and ecologically understood traits for the less studied organism groups (Paillet et al., 2010) (particularly the bryophytes in our case) makes this

approach still scarcely informative for conservation purposes compared to the use of lists of conservation-relevant species.

5 Conclusions

Our study confirms the findings from several previous studies that forest biodiversity and its response to changes in management-related environmental variables is complex. Based on our results the richness of conservation relevant species of epiphytes and saproxylic fungi appear to be suited as indicator of management impact in forests, while the richness of vascular plants, even so-called old-growth indicators, are more indicative of disturbances of natural or anthropogenic nature. This reflects the well-known notion that the mechanisms that shape patterns of diversity are not identical among species groups. Therefore a multi-taxon framework is increasingly recommended for guiding conservation action (e.g., Flensted et al., 2016; Schall et al., 2018). However, identifying species across many relevant taxonomic groups is time and resource consuming, and often impractical in broad-scale monitoring and research, while rapid assessment methods are needed for practical conservation. In this context, the identification and validation of suitable indicators of overall biodiversity and underlying ecosystem processes is key to ensure conservation that is both ecologically- and resource-efficient. The use of a functional approach has considerable potential in this context, if suitable recognisable and responsive traits can be identified (e.g., Aragón et al., 2016). For reaching this goal a preliminary selection and subsequent testing of responsive traits is required for each species group. Indeed, functional approaches depend on the compilation and evaluation of traits with documented relevance, which are only partially available, and mainly for more well studied groups. We hope future studies will improve the situation, e.g., for fungi, lichens and bryophytes, in order to identify the best suited traits which may help in effective and rapid biodiversity assessments.

Author Contributions: CL and JHC formulated the specific research hypotheses and designed the analytical setup, with input from HHB, AC, IG and JN. The overall project was formulated and coordinated by JHC, HHB, APT and CR, who also designed the field sampling protocols, with input from IG and ÖF, who collected data on ground vegetation and epiphytes respectively. CL processed and analyzed the data with help from DD and FF. CL wrote the manuscript in close collaboration with JHC, incorporating critical feedback from all authors, which helped shape the manuscript.

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References

- Aragón, G., Belinchón, R., Martínez, I., Prieto, M., 2016. A survey method for assessing the richness of epiphytic lichens using growth forms. *Ecol. Indic.* 62, 101–105. <https://doi.org/10.1016/j.ecolind.2015.11.034>.
- Aubin, I., Venier, L., Pearce, J., Moretti, M., 2013. Can a trait-based multi-taxa approach improve our assessment of forest management impact on biodiversity? *Biodivers. Conserv.* 22, 2957–2975. <https://doi.org/10.1007/s10531-013-0565-6>.
- Bardelli, T., Ascher-Jenull, J., Burkia Stocker, E., Fornasier, F., Arfaioli, P., Fravolini, G., Alves Medeiros, L.R., Egli, M., Pietramellara, G., Insam, H., Gómez-Brandón, M., 2018. Impact of slope exposure on chemical and microbiological properties of Norway spruce deadwood and underlying soil during early stages of decomposition in the Italian Alps. *Catena* 167, 100–115. <https://doi.org/10.1016/j.catena.2018.04.031>.
- Bässler, C., Cadotte, M.W., Beudert, B., Heibl, C., Blaschke, M., Bradtka, J.H., Langbehn, T., Werth, S., Müller, J., 2016a. Contrasting patterns of lichen functional diversity and species richness across an elevation gradient. *Ecography (Cop.)* 39, 689–698. <https://doi.org/10.1111/ecog.01789>.
- Bässler, C., Müller, J., Cadotte, M. W., Heibl, C., Bradtka, J. H., Thorn, S., Halbwachs, H., 2016b. Functional response of lignicolous fungal guilds to bark beetle deforestation. *Ecol. Indic.* 65, 149–160.
- Bates, D., Maechler, M., Bolker, B., Walker, S., 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* 67: 1–48. <https://cran.r-project.org/web/packages/lme4/index.html>.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manage.* 258, 525–537.
- Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manage.* 132, 39–50.
- Bibby, C. J., Burgess, N. D., Hill, D. A., Mustoe, S., 2000. *Bird Census Techniques 2nd Edition*. Academic Press. Academic Press.

- Blüthgen, N., Simons, N.K., Jung, K., Prati, D., Renner, S.C., Boch, S., Fischer, M., Hölzel, N., Klaus, V.H., Kleinebecker, T., Tschapka, M., Weisser, W.W., Gossner, M.M., 2016. Land use imperils plant and animal community stability through changes in asynchrony rather than diversity. *Nat. Commun.* 7. <https://doi.org/10.1038/ncomms10697>
- Bocci, G., 2015. TR8: an R package for easily retrieving plant species traits. *Methods Ecol. Evol.*, 6:347–350. <http://dx.doi.org/10.1111/2041-210X.12327>.
- Boch, S., Prati, D., Müller, J., Socher, S., Baumbach, H., Buscot, F., Gockel, S., Hemp, A., Hessemöller, D., Kalko, E.K.V., Linsenmair, K.E., Pfeiffer, S., Pommer, U., Schöning, I., Schulze, E.D., Seilwinder, C., Weisser, W.W., Wells, K., Fischer, M., 2013. High plant species richness indicates management-related disturbances rather than the conservation status of forests. *Basic Appl. Ecol.* 14, 496–505. <https://doi.org/10.1016/j.baae.2013.06.001>.
- Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H., White, J.S., 2009. Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol. Evol.* 24, 127–135.
- Brunet, J., Fritz, Ö., Richnau, G., 2010. Biodiversity in European beech forests – a review with recommendations for sustainable forest management. *Ecol. Bull.* 53, 77–94.
- Burrascano, S., Lombardi, F., Marchetti, M., 2008. Old-growth forest structure and deadwood: Are they indicators of plant species composition? A case study from central Italy. *Plant Biosyst.* 142, 313–323.
- Burrascano, S., Keeton, W.S., Sabatini, F.M., Blasi, C., 2013. Commonality and variability in the structural attributes of moist temperate old-growth forests: A global review. *For. Ecol. Manage.* 291, 458–479.
- Burrascano, S., Ripullone, F., Bernardo, L., Borghetti, M., Carli, E., Colangelo, M., Gangale, C., Gargano, D., Gentilesca, T., Luzzi, G., Passalacqua, N., Pelle, L., Rivelli, A.R., Sabatini, F.M., Schettino, A., Siclari, A., Uzunov, D., Blasi, C., 2017. It's a long way to the top: Plant species diversity in the transition from managed to old-growth forests. *J. Veg. Sci.* 98–109. <https://doi.org/10.1111/jvs.12588>.
- Burrascano, S., Antonini, G., Sitzia, T., Janssen, F.G.P., Blasi, C., Nascimbene, A.M.P.J., 2018. Congruence across taxa and spatial scales: Are we asking too much of species data? *Glob. Ecol. Biogeogr.* 980–990. <https://doi.org/10.1111/geb.12766>.
- Campbell, J. L., Donato, D. C., 2014. Trait-based approaches to linking vegetation and food webs in early-seral forests of the Pacific Northwest. *For. Ecol. Manage.*, 324, 172–178.
- Chaudhary, A., Burivalova, Z., Koh, L.P., Hellweg, S., 2016. Impact of Forest Management on Species Richness: Global Meta-Analysis and Economic Trade-Offs. *Sci. Rep.* 6, 1–10. <https://doi.org/10.1038/srep23954>.
- Chiarucci, A., Bacaro, G., Scheiner, S.M., 2011. Old and new challenges in using species diversity for assessing biodiversity. *Philos. Trans. R. Soc.* 366, 2426–2437.
- Christensen, M., Heilmann-Clausen, J., 2009. Forest biodiversity gradients and the human impact in Annapurna Conservation Area, Nepal. *Biodivers. Conserv.*, 18, 2205–2221.
- Christensen, M., Heilmann-Clausen, J., Walley, R., Adamcik, S., 2005. Wood-inhabiting fungi as indicators of nature value in European beech forests. *EFI Proc. No. 51 Monitoring and Indicators of Forest Biodiversity in Europe – From Ideas to Operationality*, p. 229.
- Colwell, R.K., Coddington, J. A., 1994. Estimating Terrestrial Biodiversity through Extrapolation. *Philos. Trans. R. Soc.* 345, 101–118.
- Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., Ter Steege, H., Morgan, H.D., Van Der Heijden, M.G., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Aust. J. Bot.* 51, 335–380. <https://doi.org/10.1071/BT02124>
- Curzon, M.T., D'Amato, A.W., Fraver, S., Palik, B.J., Bottero, A., Foster, J.R., Gleason, K.E., 2017. Harvesting influences functional identity and diversity over time in forests of the northeastern U.S.A. *For. Ecol. Manage.* 400, 93–99. <https://doi.org/10.1016/j.foreco.2017.05.056>.
- DOF, 2018. Danish Ornithological Society, Danmarks Fugle. <https://dofbasen.dk/ART/> (accessed 8 January 2019).
- Dolman, P.M., Panter, C.J., Mossman, H.L., 2012. The biodiversity audit approach challenges regional priorities and identifies a mismatch in conservation. *J. Appl. Ecol.* 49, 986–997. <https://doi.org/10.1111/j.1365-2664.2012.02174.x>.
- Dray, S., Dufour, A.-B., 2007. The ade4 package: Implementing the duality diagram for ecologists. *J. Stat. Softw.* 22, 1–20.
- During, H.J., 1979. Life Strategies of Bryophytes : A Preliminary Review. *Lindbergia*, 5, 2–18.
- During, H.J., 1992. Ecological classification of bryophytes and lichens. In: Bates J, Farmer A, eds. *Bryophytes and lichens in a changing environment*. Oxford: Clarendon Press, pp. 1–31.
- Ellenberg, H., 1974. *Zeigerwerte der Gefäßpflanzen Mitteleuropas*. Erich Goltze GmbH, Co KG, Göttingen, pp. 97
- Ellenberg, H., Weber, H. E., Düll, R., Wirth, V., Werner, W., Paulissen, D., 1991. *Zeigerwerte von Pflanzen in Mitteleuropa (Scripta Geobotanica 18)*. Verlag E. Goltze KG, Göttingen.
- Ellis, C.J., 2012. Lichen epiphyte diversity: A species, community and trait-based review. *Perspect. Plant Ecol. Evol. Syst.* 14, 131–152. <https://doi.org/10.1016/j.ppees.2011.10.001>.
- Emborg, J., Christensen, M., Heilmann-Clausen, J., 2000. The structural dynamics of Suserup Skov, a near-natural

- temperate deciduous forest in Denmark. *For. Ecol. Manage.* 126, 173–189.
- Fitter, A.H., Peat, H.J., 1994. The Ecological Flora Database, *J. Ecol.*, 82, 415–425. <http://www.ecoflora.co.uk>.
- Flensted, K.K., Bruun, H.H., Ejrnaes, R., Eskildsen, A., Thomsen, P.F., Heilmann-Clausen, J., 2016. Red-listed species and forest continuity - A multi-taxon approach to conservation in temperate forests. *For. Ecol. Manage.* 378, 144–159. <https://doi.org/10.1016/j.foreco.2016.07.029>.
- Fritz, Ö., 2009. Ecology and Conservation of Bryophytes and Lichens on *Fagus sylvatica*. – Doctoral Thesis No. 2009:10. Faculty of Forest Sciences, SLU.
- Fritz, Ö., Brunet, J., 2010. Epiphytic bryophytes and lichens in Swedish beech forests – effects of forest history and habitat quality. *Ecol. Bull.* 53, 95–107.
- Fritz, Ö., 2011. Lunglav minskar och bokfjädermossa ökar i Hallands bokskogar. *Svensk Bot. Tidskr.* 105, 163–177.
- Garnier, E., Cortez, J., Billes, G., Navas, M.L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.P., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecol.* 85, 2630–2637
- Garnier E., Navas M.-L., Grigulis K., 2016. Plant Functional Diversity: Organism traits, community structure, and ecosystem properties. Oxford University Press.
- Giordani, P., Brunialti, G., Bacaro, G., Nascimbene, J., 2012. Functional traits of epiphytic lichens as potential indicators of environmental conditions in forest ecosystems. *Ecol. Indic.* 18, 413–420. <https://doi.org/10.1016/j.ecolind.2011.12.006>.
- Gossner, M.M., Schall, P., Ammer, C., Ammer, U., Engel, K., Schubert, H., Simon, U., Utschick, H., Weisser, W.W., 2014. Forest management intensity measures as alternative to stand properties for quantifying effects on biodiversity. *Ecosphere* 5, art113. <https://doi.org/10.1890/ES14-00177.1>.
- Gotelli, N., Graves, G.R., Rahbek, C., 2010. Macroecological signals of species interactions in the Danish avifauna. *Proc. Natl. Acad. Sci.* 107, 5030–5035. <https://doi.org/10.1073/pnas.0914089107>.
- Gotelli, N., Colwell, R.K., 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* 4, 379–391. <https://doi.org/10.1046/j.1461-0248.2001.00230.x>.
- Graae, B. J., Buchwald, E., 1997. Særligt beskyttet naturskov - Lokalteter i Statsskovene, vol 1 Skov og Naturstyrelsen
- Graae, B.J., Sunde, P.B., 2000. The impact of forest continuity and management on forest floor vegetation evaluated by species traits. *Ecography* 23, 720–731. <https://doi.org/10.1111/j.1600-0587.2000.tb00315.x>.
- Grime J.P., 2001. *Plant Strategies, Vegetation Processes and Ecosystem Properties*, 2nd edn. Wiley.
- Hallingbäck, T., Aronsson, G. (eds.) 1998. *Ekologisk katalog över storsvampar och myxomyceter. [Macrofungi and myxomycetes of Sweden and their ecology.]* ArtDatabanken, SLU, Uppsala. 2nd revised and extended printing.
- Halme, P., Holec, J., Heilmann-Clausen, J., 2017. The history and future of fungi as biodiversity surrogates in forests. *Fungal Ecol.*, 27, 193–201.
- Heilmann-Clausen, J., Aude, E., van Dort, K., Christensen, M., Piltaver, A., Veerkamp, M., Walley, R., Siller, I., Standovár, T., Odor, P., 2014. Communities of wood-inhabiting bryophytes and fungi on dead beech logs in Europe - reflecting substrate quality or shaped by climate and forest conditions? *J. Biogeogr.* 41, 2269–2282. <https://doi.org/10.1111/jbi.12388>.
- Hermý, M., Honnay, O., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biol. Conserv.* 91, 9–22.
- Hill, M.O., Preston, C.D., Bosaquet, S.D.S., Roy, D.B., 2007. BRYOATT: Attributes of British and Irish Bryophytes.
- Julve, P., 1998. *Baseflor. Index botanique, écologique et chorologique de la flore de France.* Version: 26 November 2014. <http://perso.wanadoo.fr/philippe.julve/catminat.htm>.
- Kahl, T., Bauhus, J., 2014. An index of forest management intensity based on assessment of harvested tree volume, tree species composition and dead wood origin. *Nat. Conserv.* 7, 15–27. <https://doi.org/10.3897/natureconservation.7.7281>.
- Kassambara, A., Mundt, F., 2016. Factoextra: extract and visualize the results of multivariate data analyses. R Package. version 1.
- Kaufmann, S., Hauck, M., Leuschner, C., 2017. Comparing the plant diversity of paired beech primeval and production forests: Management reduces cryptogam, but not vascular plant species richness. *For. Ecol. Manage.* 400, 58–67. <https://doi.org/10.1016/j.foreco.2017.05.043>.
- Kleyer, M., Bekker, R.M., Knevel, I.C., Bakker, J.P., Thompson, K., Sonnenschein, M., Poschlod, P., Van Groenendael, J.M., Klimeš, L., Klimešová, J., Klotz, S., Rusch, G.M., Hermý, M., Adriaens, D., Boedeltje, G., Bossuyt, B., Dannemann, A., Endels, P., Götzenberger, L., Hodgson, J.G., Jackel, A.K., Kühn, I., Kunzmann, D., Ozinga, W.A., Römermann, C., Stadler, M., Schlegelmilch, J., Steendam, H.J., Tackenberg, O., Wilmann, B., Cornelissen, J.H.C., Eriksson, O., Garnier, E., Peco, B., 2008. The LEDA Traitbase: A database of life-history traits of the Northwest European flora. *J. Ecol.* 96, 1266–1274. <https://doi.org/10.1111/j.1365-2745.2008.01430.x>.
- Klotz, S., Kühn, I., Durka, W. (eds), 2002. *BIOLFLOR - Eine Datenbank zu biologisch-ökologischen Merkmalen zur Flora von Deutschland.* Schriftenreihe für Vegetationskunde 38, 1–333. (Bundesamt für Naturschutz).

- Kraus D., Krumm F. (eds), 2013. Integrative approaches as an opportunity for the conservation of forest biodiversity. European Forest Institute, Freiburg, Germany. 284 pp.
- Knudsen, H., Vesterholt, J., 2012. *Funga Nordica*. Agaricoid, boletoid, clavarioid, cyphelloid and gastroid genera. Nordsvamp, Denmark.
- Laliberté, E., Legendre, P., Shipley, B., 2015. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R package version 1.0–12.
- Lepš, J., de Bello, F., Lavorel, S., Berman, S., 2006. Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia* 78, 481–501.
- Mason, N.W.H., Mouillot, D., Lee, W.G., Wilson, J.B., 2005. Functional richness, functional evenness and functional divergence: The primary components of functional diversity. *Oikos* 111, 112–118. <https://doi.org/10.1111/j.0030-1299.2005.13886.x>.
- Nascimbene, J., Marini, L., 2015. Epiphytic lichen diversity along elevational gradients: Biological traits reveal a complex response to water and energy. *J. Biogeogr.* 1222–1232. <https://doi.org/10.1111/jbi.12493>.
- Nascimbene, J., Mayrhofer, H., Dainese, M., Bilovitz, P.O., 2017. Assembly patterns of soil-dwelling lichens after glacier retreat in the European Alps. *J. Biogeogr.* 44, 1393–1404. <https://doi.org/10.1111/jbi.12970>.
- Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Sekercioglu, Ç.H., Alkemade, R., Booth, H., Purves, D.W., 2012. Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proc R Soc B* 280, 1–8. <https://doi.org/10.1098/rspb.2012.2131>.
- Nimis, P.L., Martellos, S., 2017. ITALIC - The Information System on Italian Lichens. Version 5.0. University of Trieste, Dept. of Biology. <http://dryades.units.it/italic>.
- Nitare, J., 2000. Indicator species for assessing the nature conservation value of woodland sites: a flora of selected cryptogams [in Swedish]. Skogstyrelsen, Karlshamn, 384 pp.
- Nordén, J., Penttilä, R., Siitonen, J., Tomppo, E., Ovaskainen, O., 2013. Specialist species of wood-inhabiting fungi struggle while generalists thrive in fragmented boreal forests. *J. Ecol.* 101, 701–712.
- Nordén, B., Dahlberg, A., Brandrud, T.E., Fritz, Ö., Ejrnæs, R., Ovaskainen, O., 2014. Effects of ecological continuity on species richness and composition in forests and woodlands: A review. *Écoscience* 21, 34–45. <https://doi.org/10.2980/21-1-3667>.
- Ódor, P., Király, I., Tinya, F., Bortignon, F., Nascimbene, J., 2014. Patterns and drivers of species composition of epiphytic bryophytes and lichens in managed temperate forests. *For. Ecol. Manage.* 321, 42–51. <https://doi.org/10.1016/j.foreco.2014.01.035>.
- Overballe-Petersen, M.V., Nielsen, A.B., Hannon, G.E., Halsall, K., Bradshaw, R.H.W., 2013. Long-term forest dynamics at Gribskov, eastern Denmark with early-Holocene evidence for thermophilous broadleaved tree species. *Holocene* 23, 243–254.
- Paillet, Y., Bergès, L., Hjaltén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Mészáros, I., Sebastià, M.T., Schmidt, W., Standovár, T., Tothmérész, B., Uotila, A., Valladares, F., Vellak, K., Virtanen, R., 2010. Biodiversity differences between managed and unmanaged forests: Meta-analysis of species richness in Europe. *Conserv. Biol.* 24, 101–112. <https://doi.org/10.1111/j.1523-1739.2009.01399.x>
- Pausas, J.G., Verdú, M., 2010. The jungle of methods for evaluating phenotypic and phylogenetic structure of communities. *Bioscience* 60, 614–625. <https://doi.org/10.1525/bio.2010.60.8.7>.
- Pouska, V., Macek, P., Zíbarová, L., 2016. The relation of fungal communities to wood microclimate in a mountain spruce forest. *Fungal Ecol.*, 21, 1–9.
- R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna. URL: <https://www.R-project.org/>.
- Roberts, M. R., 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany*, 82, 1273–1283.
- Rune, F., 2009. Gribskov - Skovens udvikling og kulturhistorie fra istid til nutid. Forlaget Esrum Sø, Fredensborg, 357 pp.
- Ricotta, C., Moretti, M., 2011. CWM and Rao's quadratic diversity: A unified framework for functional ecology. *Oecologia* 167, 181–188. <https://doi.org/10.1007/s00442-011-1965-5>.
- Ryvarden, L., Melo, I., Niemelä, T., 2014. Poroid Fungi of Europe, vol 31, Synopsis Fungorum. Fungiflora, Oslo.
- Sabatini, F.M., Burrascano, S., Azzella, M.M., Barbati, A., De Paulis, S., Di Santo, D., Facioni, L., Giuliarelli, D., Lombardi, F., Maggi, O., Mattioli, W., Parisi, F., Persiani, A., Ravera, S., Blasi, C., 2016. One taxon does not fit all: Herb-layer diversity and stand structural complexity are weak predictors of biodiversity in *Fagus sylvatica* forests. *Ecol. Indic.* 69, 126–137. <https://doi.org/10.1016/j.ecolind.2016.04.012>.
- Sabatini, F., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., Debaive, N., Horváth, F., Garbarino, M., Grigoriadis, N., Lombardi, F., Duarte, I.M., Meyer, P., Midteng, R., Mikac, S., Mikoláš, M., Motta, R., Mozgeris, G., Nunes, L., Panayotov, M., Ódor, P., Ruete, A., Simovski, B., Stillhard, J., Svoboda, M., Szwagrzyk, J., Tikkanen, O.-P., Volosyanichuk, R., Vrska, T., Zlatanov, T., Kuemmerle, T., 2018. Where are Europe's last primary forests? *Divers. Distrib.* 1–14. <https://doi.org/10.1111/ddi.12778>.

- Schall, P., Gossner, M.M., Heinrichs, S., Fischer, M., Boch, S., Prati, D., Jung, K., Baumgartner, V., Blaser, S., Böhm, S., Buscot, F., Daniel, R., Goldmann, K., Kaiser, K., Kahl, T., Lange, M., Müller, J., Overmann, J., Renner, S.C., Schulze, E.D., Sikorski, J., Tschapka, M., Türke, M., Weisser, W.W., Wemheuer, B., Wubet, T., Ammer, C., 2018. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *J. Appl. Ecol.* 55, 267–278. <https://doi.org/10.1111/1365-2664.12950>.
- Schmidt, M., Mölder, A., Schönfelder, E., Engel, F., Schmiedel, I., Culmsee, H., 2014. Determining ancient woodland indicator plants for practical use: A new approach developed in northwest Germany. *For. Ecol. Manage.* 330, 228–239. <https://doi.org/10.1016/j.foreco.2014.06.043>.
- Šebesta, J., Maděra, P., Řepka, R., Matula, R., 2017. Comparison of vascular plant diversity and species composition of coppice and high beech forest in the Banat region, Romania. *Folia Geobot.* 52, 33–43. <https://doi.org/10.1007/s12224-016-9279-3>.
- Simmel, J., Bässler, C., Poschlod, P., 2017. Ellenberg indicator values for macromycetes – a methodological approach and first applications. *Fungal Ecol.* 27, 202–212. <https://doi.org/10.1016/j.funeco.2016.09.004>.
- Sitzia, T., Campagnaro, T., Dainese, M., Cassol, M., Cortivo, M., Gatti, E., Padovan, F., Sommacal, M., Nascimbene, J., 2017. Contrasting multi-taxa diversity patterns between abandoned and non-intensively managed forests in the southern Dolomites. *iForest - Biogeosciences For.* 10, 845–850. <https://doi.org/10.3832/ifor2181-010>.
- Standovár, T., Ódor, P., Aszalós, R., Gálhidy, L., 2006. Sensitivity of ground layer vegetation diversity descriptors in indicating forest naturalness. *Community Ecol.* 7, 199–209. <https://doi.org/10.1556/ComEc.7.2006.2.7>.
- Svensson, L., Mullarney, K., Zetterstrom, D., Grant, P. J., Christie, D.A., 2010. *Collins Bird Guide: The Most Complete Guide to the Birds of Britain and Europe*. Collins, second edn.
- Thor, G., Arvidsson, L. (red.). 1999. Rödlistade lavar i Sverige – Artfakta. ArtDatabanken, SLU, Uppsala.
- Violle, C., Navas, M., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! *Oikos* 1–11. <https://doi.org/10.1111/j.2007.0030-1299.15559.x>.
- Wind, P., Pihl, S. (eds.), 2004. *The Danish Red List*. - The National Environmental Research Institute, Aarhus University - redlist.dmu.dk (updated April 2010).
- Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. *For. Ecol. Manage.* 255, 1251–1261. <https://doi.org/10.1016/j.foreco.2007.10.029>.
- Wirth, V., 2010. Ökologische Zeigerwerte von Flechten - Erweiterte und Aktualisierte Fassung. *Herzogia*, 23, 229–248.

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