UNIWERSYTET RZESZOWSKI
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Wieloletnie przemiany roślinności runa lasów bukowych w polskiej części Karpat Wschodnich w związku z rozwojem drzewostanów i ich użytkowaniem

Rozprawa doktorska wykonana w Instytucie Biologii i Biotechnologii pod kierunkiem dr hab. Tomasza Duraka, prof. UR.

Dziedzina nauki ścisłe i przyrodnicze

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SPIS TREŚCI

Oświadczenia współautorów

Publikacje wchodzące w skład rozprawy doktorskiej wraz z suplementami

1. INFORMACJE WPROWADZAJĄCE

1.1. Publikacje wchodzące w skład rozprawy doktorskiej

1. **Bugno-Pogoda, A.**, Durak, R., Durak, T. 2021. Impact of Forest Management on the Temporal Dynamics of Herbaceous Plant Diversity in the Carpathian Beech Forests over 40 Years. *Biology*, 10: 406. **(IF$_{2021}$ = 5,079; Punkty MNiSW$_{2021}$ = 100)**

2. **Bugno-Pogoda, A.**, Durak, T. 2021. Climate and Management Factors Underlying Changes in Beech Forest Herbaceous Layer Plant Communities in the Polish Eastern Carpathians. *Forests*, 12: 1446. **(IF$_{2021}$ = 2,634; Punkty MNiSW$_{2021}$ = 100)**

3. Durak, T., **Bugno-Pogoda, A.**, Durak, R. 2022. Impact of forest stand development on long-term changes in the herb layer of semi-natural Carpathian beech forests. *Forest Ecology and Managament*, 518: 120233. **(IF$_{2021}$ = 3,558; Punkty MNiSW$_{2021}$ = 200)**

Sumaryczna wartość współczynnika **Impact Factor** publikacji wchodzących w skład rozprawy doktorskiej (zgodnie z rokiem opublikowania) wynosi **11,271** (**400** punktów **MNiSW**).

1.2. Pozostałe publikacje

1. Durak, T., **Bugno-Pogoda, A.**, Durak, R. 2021. Application of forest inventories to assess the forest developmental stages on plots dedicated to long-term vegetation studies. *Forest Ecology and Managament*, 489: 119041. **(IF$_{2021}$ = 3,558; Punkty MNiSW$_{2021}$ = 200)**
2. **Bugno-Pogoda A.**, Durak T. 2019. Zmiany składu gatunkowego i różnorodności leśnych zbiorowisk roślin zielnych w gospodarczych lasach bukowych. 58. Zjazd Polskiego Towarzystwa Botanicznego. Botanika bez granic. Kraków 2019, s. 82.
3. **Bugno-Pogoda A.**, Durak T. 2018. Zrównoważony rozwój w leśnictwie. *Polish Journal for Sustainable Development*. 22 (1). Rzeszów 2018, s.7-12. **(IF$_{2018}$ = - ; Punkty MNiSW$_{2018}$ = 6**)
4. **Bugno-Pogoda A.**, Durak T. 2017. Obszary Natura 2000 na gruntach zarządzanych przez Lasy Państwowe. Ogólnopolska konferencja naukowa „NATURALni 2017”. Zbiór artykułów z Konferencji naukowych „NATURALni 2017” oraz „Nauka Ściśle Tajna”. Fundacji Promovendi. Łódź 2017, s.14-18. (rozdział w monografii)

5. **Bugno-Pogoda A.**, Durak T. 2017. Olejki eteryczne z leśnych surowców olejkodajnych. Wybrane substancje o znaczeniu biologicznym - Spojrzenie młodych naukowców. Creativetime. Kraków 2017, s. 67-73. (rozdział w monografii)
6. **Bugno-Pogoda A.**, Dudek T., Durak T. 2016. Rola lasów w kształtowaniu gospodarki wodnej. Spojrzenie młodych naukowców na rozwój nauk biologicznych i chemicznych. Materiały Pokonferencyjne. Creativetime. Kraków 2016, s.7-8. (rozdział w monografii)

Sumaryczna wartość współczynnika **Impact Factor** dorobku publikacyjnego łącznie z publikacjami wchodzącymi w skład rozprawy doktorskiej (wg opublikowania) wynosi **14,829 (606** punktów **MNiSW**).

1.3. Komunikaty zjazdowe

1. **Bugno-Pogoda A.** *Zmiany składu gatunkowego i różnorodności leśnych zbiorowisk roślin zielnych w gospodarczych lasach bukowych*. 58. Zjazd Polskiego Towarzystwa Botanicznego. Botanika bez granic. Polska, Kraków 1-7.07.2019. (prezentacja posterowa).
2. **Bugno-Pogoda A.**, Durak T. *Obszary Natura 2000 na gruntach zarządzanych przez Lasy Państwowe.* Ogólnopolska konferencja naukowa „NATURALni 2017”. Polska, Łódź, 11.03.2017. (prezentacja ustna).
3. **Bugno-Pogoda A.** *Zrównoważony rozwój w leśnictwie.* III Konferencja Naukowa pt. DEKADA RÓŻNORODNOŚCI BIOLOGICZNEJ. Polska, Rzeszów, 05.12.2017. (prezentacja posterowa).
4. **Bugno-Pogoda A.**, Dudek T., Durak T. *Rola lasów w kształtowaniu gospodarki wodnej.* Nauki biologiczne i chemiczne. Spojrzenie młodych naukowców. Polska, Kraków, 22.10.2016. (prezentacja posterowa).

1.4. Udział w projektach badawczych

Tytuł projektu badawczego: „Analiza i opracowanie wyników inwentaryzacji stanu lasów Regionalnej Dyrekcji Lasów Państwowych w Krośnie”

Charakter udziału w projekcie badawczym: **wykonawca (prace analityczne)**

Źródło finansowania: Państwowe Gospodarstwo Leśne Lasy Państwowe

Kierownik projektu: dr inż. Bożydar Neroj, mgr inż. Bogumił Dąbek

Okres trwania projektu (lata): 2021-2022

1.5. Opracowania

1. Opracowanie fitosocjologiczne leśnych zbiorowisk roślinnych dla Nadleśnictwa Stuposiany „LKP Lasy Bieszczadzkie”. BULiGL. Przemyśl, 2014.
2. Opracowanie fitosocjologiczne leśnych zbiorowisk roślinnych dla Nadleśnictwa Lutowiska obrębu Dwernik „LKP Lasy Bieszczadzkie”. BULiGL. Przemyśl, 2014.
3. Elaborat siedliskowy Nadleśnictwa Stuposiany. BULiGL. Przemyśl, 2014.
4. Elaborat siedliskowy Nadleśnictwa Lutowiska obręb Dwernik. BULiGL. Przemyśl, 2014.
5. Elaborat siedliskowy Nadleśnictwa Komańcza obręb Łupków. BULiGL. Przemyśl, 2015.
6. Elaborat siedliskowy Nadleśnictwa Baligród obręb Bukowiec. BULiGL. Przemyśl, 2015.
7. Elaborat siedliskowy Nadleśnictwa Jarosław. BULiGL. Przemyśl, 2016.
8. Elaborat siedliskowy Nadleśnictwa Oleszyce. BULiGL. Przemyśl, 2016.
9. Program ochrony przyrody dla Nadleśnictwa Jarosław. BULiGL. Przemyśl, 2016.
10. Prognoza oddziaływania na środowisko Planu Urządzenia Lasu Nadleśnictwa Jarosław wg stanu na dzień 1 stycznia 2017 r. BULiGL. Przemyśl, 2016.
11. Program ochrony przyrody dla Nadleśnictwa Oleszyce. BULiGL. Przemyśl, 2016.
12. Zadania ochronne dla obszarów Natura 2000 w ramach PUL w: Program ochrony przyrody dla Nadleśnictwa Brzozów. BULiGL. Przemyśl, 2017.
13. Zadania ochronne dla obszarów Natura 2000 w ramach PUL oraz Program ochrony przyrody dla Nadleśnictwa Rymanów. BULiGL. Przemyśl, 2018.
14. Zadania ochronne dla obszarów Natura 2000 w ramach PUL dla Nadleśnictwa Ustrzyki Dolne. BULiGL. Przemyśl, 2018.
15. Zadania ochronne dla obszarów Natura 2000 w ramach PUL dla Nadleśnictwa Lesko. BULiGL. Przemyśl, 2018.
16. Zadania ochronne dla obszarów Natura 2000 oraz Program ochrony przyrody dla Nadleśnictwa Krasiczyn. BULiGL. Przemyśl, 2018.
17. Prognoza oddziaływania na środowisko Planu Urządzenia Lasu Nadleśnictwa Krasiczyn wg stanu na dzień 1 stycznia 2019 r. BULiGL. Przemyśl, 2018.
18. Program ochrony przyrody dla Nadleśnictwa Tomaszów. BULiGL. Przemyśl, 2019.
19. Prognoza oddziaływania na środowisko Planu Urządzenia Lasu Nadleśnictwa Tomaszów wg stanu na dzień 1 stycznia 2020 r. BULiGL. Przemyśl, 2019.

20. Ekspertyza dotycząca możliwości kompensacji przyrodniczej zajęcia siedlisk przyrodniczych w związku z silną presją inwestycyjną oraz oczekiwaniami społecznymi na obszarze Natura 2000 Bieszczady PLC180001, niezbędnej do zapewnienia spójności i właściwego funkcjonowania sieci obszarów Natura 2000. BULiGL. Przemyśl, 2019.
21. Program ochrony przyrody dla Nadleśnictwa Kolbuszowa. BULiGL. Przemyśl, 2020.
22. Prognoza oddziaływania na środowisko Planu Urządzenia Lasu dla Nadleśnictwa Kolbuszowa wg stanu na dzień 1 stycznia 2021 r. BULiGL. Przemyśl, 2020.
23. Sprawozdanie z prac monitoringowych wykonanych w 2021 roku ramach umowy nr 15 POIS-0015/18-00 z dnia 19 marca 2021 roku, obejmującej monitoring skuteczności zabiegów w ekosystemach torfowiskowych. W ramach projektu „Czynna ochrona zagrożonych gatunków i siedlisk w ekosystemach nieleśnych Bieszczadzkiego Parku Narodowego w latach 2019-2023.” W ramach działania 2.4., oś priorytetowa II Programu Operacyjnego Infrastruktura i Środowisko 2014-2020. BULiGL. Przemyśl, 2021.
24. Raport z wykonania ekspertyzy przyrodniczej na potrzeby uzupełnienia stanu wiedzy o przedmiotach ochrony w obszarach Natura 2000 województwa lubelskiego. Izbicki Przełom Wieprza PLH060030 - weryfikacja granic obszaru pod kątem występowania siedliska: murawy kserotermiczne *Festucu-Brometea* 6210 oraz innych siedlisk przyrodniczych i gatunków mogących mieć znaczenie dla ochrony obszaru. W ramach projektu: POIS.02.04.00-00-0191/16 pn. Inwentaryzacja cennych siedlisk przyrodniczych kraju, gatunków występujących w ich obrębie oraz stworzenie Banku Danych o Zasobach Przyrodniczych, współfinansowanego przez Unię Europejską ze środków Funduszu Spójności w ramach Programu Operacyjnego Infrastruktura i Środowisko 2014-2020.
25. Raport dotyczący opracowania fitosocjologicznego w ramach tematu badawczego „Analiza i ocena stanu lasów Regionalnej Dyrekcji Lasów Państwowych w Krośnie z uwzględnieniem Parków Narodowych: Bieszczadzkiego, Magurskiego i Roztoczańskiego oraz rezerwatów przyrody, w oparciu o wyniki inwentaryzacji przyrodniczo-kulturowej”. Praca wykonania na zlecenie Dyrekcji Generalnej Lasów Państwowych w ramach umowy nr EZ.271.3.15.2021 z dnia 29 października 2021 r.

2. STRESZCZENIE

Na rozprawę doktorską składa się cykl trzech prac opublikowanych w czasopismach *Biology*, *Forests* oraz *Forest Ecology and Management* poświęconych (1) wpływie gospodarki leśnej na czasową dynamikę różnorodności roślin zielnych w buczynie karpackiej na przestrzeni ponad 40 lat, (2) czynnikom dotyczącym struktury lasu i klimatu, które mają wpływ na zmiany zachodzące w roślinności zielnej w buczynie karpackiej, (3) wpływie rozwoju drzewostanów na długookresowe zmiany w warstwie zielnej w półnaturalnej buczynie karpackiej.

Wieloletnie przemiany roślinności runa lasów bukowych w polskiej części Karpat Wschodnich w związku z rozwojem drzewostanów i ich użytkowaniem na przestrzeni ponad 40 lat przeanalizowano na podstawie danych fitosocjologicznych z powierzchni badawczych zlokalizowanych w Górach Sanocko-Turczańskich (lata 1970., 2000., 2010.). Powierzchnie te znajdywały się w lasach będących w zarządzie Nadleśnictwa Brzozów, Lesko i Ustrzyki Dolne. Dane ze zdjęć fitosocjologicznych uzupełniono o dane z inwentaryzacji drzewostanów sporządzonych na potrzeby Planów Urządzenia Lasu. W analizach uwzględniono również dane klimatyczne (średnia temperatura i suma opadów w okresie wegetacyjnym) zarejestrowane przez stację meteorologiczną w Lesku. Skupiono się na przemianach jakie zaszły w roślinności runa na tle zmian w strukturze starzejących się drzewostanów. W szczególności przeanalizowano dynamikę zmian kompozycji gatunkowej i różnorodności roślinności w odniesieniu do stadiów rozwojowych drzewostanu i prowadzonej gospodarki leśnej.

Na przestrzeni lat wzrosła lesistość, zmniejszyła się fragmentacja lasów. Wprowadzono mniej inwazyjne sposoby zagospodarowania lasów, a pozaprodukcyjne użytkowanie przez ludność zmalało. Zmieniła się struktura wiekowa i przestrzenna drzewostanów. Zmiana stosowanej rębni z częściowej na stopniową zapoczątkowała kształtowanie drzewostanów o złożonej strukturze pionowej. Jednocześnie, w ostatnim okresie badań nasiliły się procesy pozyskiwania drewna w związku z odnawianiem drzewostanu. Wymienione procesy wpływały na zmianę warunków świetlnych i wilgotnościowych panujących na dnie lasu między okresami badań, co dało się zauważyć w zmianie składu gatunkowego roślinności zielnej.

Średnia frekwencja gatunków na poziomie zbiorowiska była najwyższa w latach 2000., a w latach 2010. najniższa. Podobne wyniki otrzymano analizując średnie bogactwo gatunkowe na poziomie powierzchni badawczej. Ogólnie w latach 2010. średnia liczba gatunków w wyróżnionych grupach była mniejsza niż w poprzednich okresach badawczych. Na przestrzeni lat nie zmieniła się liczba gatunków porębowych, jednak istotnie wzrosło ich pokrycie.

Ogólny spadek liczby gatunków w 2010. powiązano z faktem starzenia się buczyn, większą intensywnością działań gospodarczych w drzewostanach będących w stadium terminalnym, konkurencją ze strony podrostu i podszytu oraz mniejszą wilgotnością gleby. Wśród roślin zielnych w okresie badań 2010. odnotowano mniejszy udział gatunków o strategii życiowej C, oraz większy udział gatunków o strategii S.

Zmiana różnorodności gatunkowej na przestrzeni lat była dość wyraźna. Różnorodność alfa była największa w 2000. a najmniejsza w 2010. Beta różnorodność była największa w 2010. a najmniejsza w 2000.

W każdym okresie badawczym wyróżniono i scharakteryzowano trzy szeroko ujęte stadia rozwojowe drzewostanu: dorastania, optymalne i terminalne. Analiza roślinności zielnej wykazała istnienie różnic w kompozycji gatunkowej i różnorodności między tymi stadiami. W stadium optymalnym odnotowano najwyższą różnorodność alfa i najniższą różnorodność beta, natomiast w stadium dorastania i terminalnym różnorodność beta była wysoka. W roślinności zielnej stadium optymalnego stwierdzono dominację strategii C. Prawdopodobnie dominacja ta jest efektem wysokiej stabilności siedliskowej tego etapu rozwoju lasu.

Wyniki przedstawione w pracy wskazują na istotny wpływ etapu rozwoju drzewostanów na przemiany zachodzące w kompozycji gatunkowej i różnorodności roślinności runa lasów bukowych polskiej części Karpat Wschodnich.

3. ABSTRACT

The doctoral dissertation consists of a series of three works published in the journals *Biology*, *Forests* and *Forest Ecology and Management* devoted to (1) the impact of forest management on the temporal dynamics of herbaceous plant diversity in the Carpathian beech forest over 40 years, (2) the factors related to the structure of the forest and climate which have an impact on changes in herbaceous plants in the Carpathian beech forest, (3)

the impact of the development of stands on long-term changes in the herbaceous layer in the semi-natural Carpathian beech forest.

The long-term changes in the vegetation of the herbaceous plants of beech forests in the Polish part of the Eastern Carpathians connected to the development of stands and their use over 40 years were analyzed based on phytosociological relevés from semi-permanent sampling plots located in the Sanocko-Turczańskie Mountains (1970s, 2000s, 2010s). These sampling plots were located in forests managed by the Forest Districts of Brzozów, Lesko and Ustrzyki Dolne. The data from phytosociological relevés was supplemented with data from the inventory of stands prepared for the forest management plans. The analysis also took into account climatic data (average temperature and precipitation during the growing season) recorded by the meteorological station in Lesko. The focus was on the changes in the herbaceous layer of plants against the changes in the structure of aging stands. In particular, the dynamics of changes in the species composition and diversity of vegetation in relation to the development stages of the stand and forest management were analyzed.

Over the years, forest cover has increased and forest fragmentation has decreased. Less invasive methods of forest management were introduced, and non-productive use by the population decreased. The age and spatial structure of the stands has changed. Conversion from the regular shelterwood system to the irregular shelterwood system initiated the development of stands with complex overstorey structure. At the same time, in the last period of the research, the processes of cutting trees intensified in connection with the regeneration period of the stand. The aforementioned processes altered the lighting and moisture conditions of the forest floor between the research periods, which was noticeable in the change in the herbaceous plant species composition.

The average frequency of species at the community level was the highest in the 2000s, and the lowest in 2010s. Similar results were obtained when analyzing the average species richness at the level of the sampling plot. In general, in 2010, the average number of species in the distinguished groups was lower than in the previous research periods. Over the years, the number of species associated with forest clearings has not changed, but their coverage has increased significantly.

The overall decline of species in 2010s has been linked to the aging of beech forests, greater intensity of management in terminal stage of forests, competition of the shrub layer, and lower soil moisture. Among herbaceous plants, in the research period of 2010s, there was a lower share of species with a plant strategy C, and a greater share of species with a plant strategy S.

The change in species diversity over the years was quite noticable. Alpha diversity was highest in 2000s and lowest in 2010s. Beta diversity was highest in 2010s and lowest in 2000s.

In each research period, three broadly defined development stages of the stand were distinguished and characterized: growing, optimum and terminal. The analysis of herbaceous plants revealed differences in species composition and diversity between these stages. At the optimum stage, the highest alpha diversity and the lowest beta diversity were recorded, while in the adolescent and terminal stages, beta diversity was high. Strategy C was dominant in the herbaceous plants of the optimum stage. This dominance is probably the result of the high habitat stability of this stage of forest development.

The results presented in the doctoral dissertation show a significant influence of the stage of development of stands on the changes taking place in the species composition and vegetation diversity of the herbaceous layer of plants of beech forests in the Polish part of the Eastern Carpathians.

4. WSTĘP

Drzewostan jest jednym z głównych czynników kształtujących warunki abiotyczne w lesie. Cechy drzewostanu takie jak struktura pionowa i pozioma, różnorodność gatunkowa, wskaźnik zadrzewienia, ilość martwego drewna silnie wpływają na skład gatunkowy i różnorodność organizmów zasiedlających wnętrze lasu (Aussenac 2000; Augusto i in. 2003; Ritter i in. 2005; Grgic i Kos 2005; Barbier i in. 2008; Winter i Brambach, 2011; Larrieu i in. 2014; Begehold i in. 2015). Zarówno w lasach naturalnych jak i w lasach gospodarczych struktura drzewostanu podlega cyklicznym zmianom, będących podstawą do wyodrębnienia stadiów rozwojowych (Watt 1947; Koop 1989; Leibundgut 1993; Korpel 1995; Meyer 1999; Tabaku 2000; Standovar i Kenderes 2003). Wraz z przejściem drzewostanu z jednego do kolejnego stadium rozwojowego zmieniają się warunki abiotyczne kształtujące warstwę zielną (Van Calster i in. 2007; Dittrich i in. 2012; Ujházy i in. 2017). W efekcie na różnym etapie rozwoju drzewostanu, różne gatunki roślin zielnych osiągają swoje optima ekologiczne (Ujházy i in. 2005, 2017).

Dotychczasowe dane z archiwalnych inwentaryzacji roślinności (zdjęć fitosocjologicznych wykonywanych metodą Braun-Blanqueta (1964)) nie zawierają informacji o stadium rozwojowym drzewostanu, ani informacji pozwalających na określenie tego stadium. Uzupełnienie zapisów inwentaryzacji roślinności leśnej o bogaty zestaw danych dotyczących struktury drzewostanów jest możliwe dzięki wykorzystaniu opisów z inwentaryzacji lasu wykonywanej na potrzeby sporządzania tzw. Planów Urządzenia Lasu (Durak i in. 2021). W Polsce dokumenty te dotyczą lasów zarządzanych przez Lasy Państwowe i zawierają szczegółowy opis drzewostanów z poszczególnych wydzieleń leśnych. Inwentaryzacje wykonywane są co dziesięć lat przez wykwalifikowanych specjalistów. Pierwsze, pełne dane pochodzą z lat 70-tych ubiegłego wieku. W niniejszej pracy, w analizach zmian zachodzących w leśnej roślinności zielnej uwzględniono stadia rozwojowe lasu określone na podstawie zmiennych drzewostanowych pochodzących z tradycyjnych inwentaryzacji roślinności (zdjęć fitosocjologicznych) oraz inwentaryzacji lasu.

Od drugiej połowy XX wieku w składzie gatunkowym europejskich leśnych zbiorowisk roślinnych nastąpiły zmiany, które często były identyfikowane jako zagrożenie dla funkcjonowania zbiorowisk i ekosystemów, a także prowadziły do utraty bioróżnorodności (Bengtsson i in. 2000; Rackham 2008; Perring i in. 2018). Powodem były zmieniające się globalnie warunki środowiskowe (zmiany klimatyczne, zanieczyszczenie powietrza), a także oddziaływania lokalne, jak gospodarka leśna oraz uboczne użytkowanie lasu np. zbieranie drewna na opał czy grabienie ściółki (Bürgi i in. 2015; Franklin i in. 2016).

Najbardziej wiarygodnym sposobem poznania odpowiedzi roślinności na zmiany zachodzące w środowisku są badania długoterminowe (Van Calster i in. 2007; De Lombaerde i in. 2018). Wymagają one użycia powtarzalnej metody, a także dużego zaangażowania ze strony kolejnych badaczy (Faliński 2012). Dotychczasowa wiedza na temat zależności między zmianami w strukturze i zagospodarowaniu lasu, a kompozycją gatunkową i różnorodnością roślinności zielnej opierała się bardzo często na danych pochodzących z dwóch okresów badawczych (Van Calster i in. 2007; Baeten i in. 2009; Durak i Durak 2015; Heinrichs i Schmidt 2017). Ponadto wpływ stopnia rozwoju drzewostanów i gospodarki leśnej na różnorodność gatunkową roślin zielnych badano uwzględniając najczęściej jedynie różnorodność alfa wyrażoną bogactwem gatunkowym (Gotelli i in. 2001; Paillet i in. 2010; Chaudhary i in. 2016). Uzyskane w tych pracach wyniki umożliwiały śledzenie zmian zachodzących w roślinności zielnej między początkowym i końcowym terminem badań sugerując, że mają one charakter kierunkowy. Uwzględnienie większej ilości terminów badań może wykazać, że zachodzące w roślinności zmiany mogą być procesem o charakterze fluktuacji lub cyklicznym.

Przed II wojną światową lasy w Polsce były mocno eksploatowane. Pozyskanie drewna przekraczało jego przyrost, wycinano głównie najstarsze drzewostany na rozległych powierzchniach, często z zastosowaniem rębni zupełnych (Majchrowska 2018). W polskiej części Karpat Wschodnich dopiero pomiędzy rokiem 1950 a 1990 zaczęto stosować rębnie częściowe (podczas których okres regeneracji drzewostanu wynosił 10-20 lat, w skutek czego powstawały jednopiętrowe drzewostany, o niewielkim zróżnicowaniu wiekowym). Następnie w drugiej połowie lat 90. rębnie częściowe zastąpiono rębniami stopniowymi (Jaworski i Kołodziej 2004; Jaworski 2018). Prowadzenie rębni stopniowych w których okres odnowienia wynosi 30-50 lat, daję szansę na wytworzenie drzewostanów o złożonej strukturze piętrowej i znacznym zróżnicowaniu wiekowym. Wiąże się to również z rozłożonymi w długim czasie zmianami ilości światła docierającego do dna lasu. Sposób zagospodarowania lasu (wielkość powierzchni objętej cięciami, rodzaj stosowanej rębni, długość okresu odnowienia) ma znaczący wpływ na różnorodność roślinności runa ponieważ krótko lub długotrwale zmienia warunki siedliskowe (głównie ilość światła docierającą do dna lasu i wilgotność), a także warunki sprzyjające lub ograniczające rozprzestrzenianie się nasion (Helmy i in. 2017; Jacob i in. 2009; Ujházy i in. 2017). Nie bez znaczenia dla roślinności zielnej w lasach bukowych wydaje się mieć również konkurencyjne oddziaływanie zwarcie rosnącego w gniazdach podrostu (głównie bukowego). Gatunek ten jest silnym konkurentem o składniki odżywcze i wodę (Ellenberg i Leuschner 2010).

Ważnym czynnikiem wpływającym na leśne zbiorowiska roślin zielnych są zmiany klimatyczne. W ubiegłych dziesięcioleciach wpływ zmian klimatu na europejskie lasy bukowe rozpatrywany był przede wszystkim w kontekście zmian w strukturze drzewostanów. Stwierdzono, że zróżnicowana struktura drzewostanów może polepszyć ich stabilność podczas zmian klimatycznych (Parpan i in. 2013; Bosela i in. 2016; Vacek i in. 2017, 2019; Krupková i in. 2019). W Karpatach w latach 1881-2009 odnotowano wzrost średniej rocznej temperatury o około 1,6 °C (Melo i in. 2013). Wyższe temperatury powodują szybsze nagrzewanie się gleby, a to wpływa na wcześniejsze rozpoczęcie wegetacji roślin zielnych, zwiększenie w zbiorowiskach udziału gatunków termofilnych (Heinrichs i in. 2012; Zellweger i in. 2020). W ostatnich kilkunastu latach w Europie środkowej odnotowano spadek średniej sumy opadów przekładający się na mniejszą wilgotność wierzchniej warstwy gleby (Felsmann i in. 2018). W lasach zwarta warstwa koron drzew i krzewów pełni rolę buforującą zmiany zachodzące w makroklimacie (Bosela i in. 2016). Stąd wydaje się, że leśny mikroklimat, który ma szczególne znaczenie dla funkcjonowania roślinności zielnej może być zaburzony na skutek przerzedzenia koron drzew (np. w wyniku rozwoju drzewostanu lub gospodarki leśnej), co będzie skutkować zwiększeniem temperatury na dnie lasu i spadkiem wilgotności gleby (Thom i in. 2020; Zellweger i in. 2020).

5. CELE PRACY I HIPOTEZY BADAWCZE

Celem cyklu prac wykonanych w ramach przygotowania rozprawy doktorskiej była:

(1) analiza przebiegu zmian w kompozycji gatunkowej i różnorodności roślinności runa lasów bukowych w polskich Karpatach Wschodnich na przestrzeni ponad 40 lat;

(2) diagnoza zmian w kompozycji gatunkowej i różnorodności roślinności runa lasów bukowych w wyniku rozwoju drzewostanów i prowadzonej gospodarki leśnej;

(3) ocena wpływu rozwoju drzewostanów i ich użytkowania na przebieg długoterminowych zmian roślinności zielnej.

Ponadto, w analizie długoterminowych przemian roślinności zielnej w kontekście rozwoju drzewostanów podjęto próbę uwzględnienia wpływu zmian klimatu.

Postawiono następujące hipotezy badawcze:

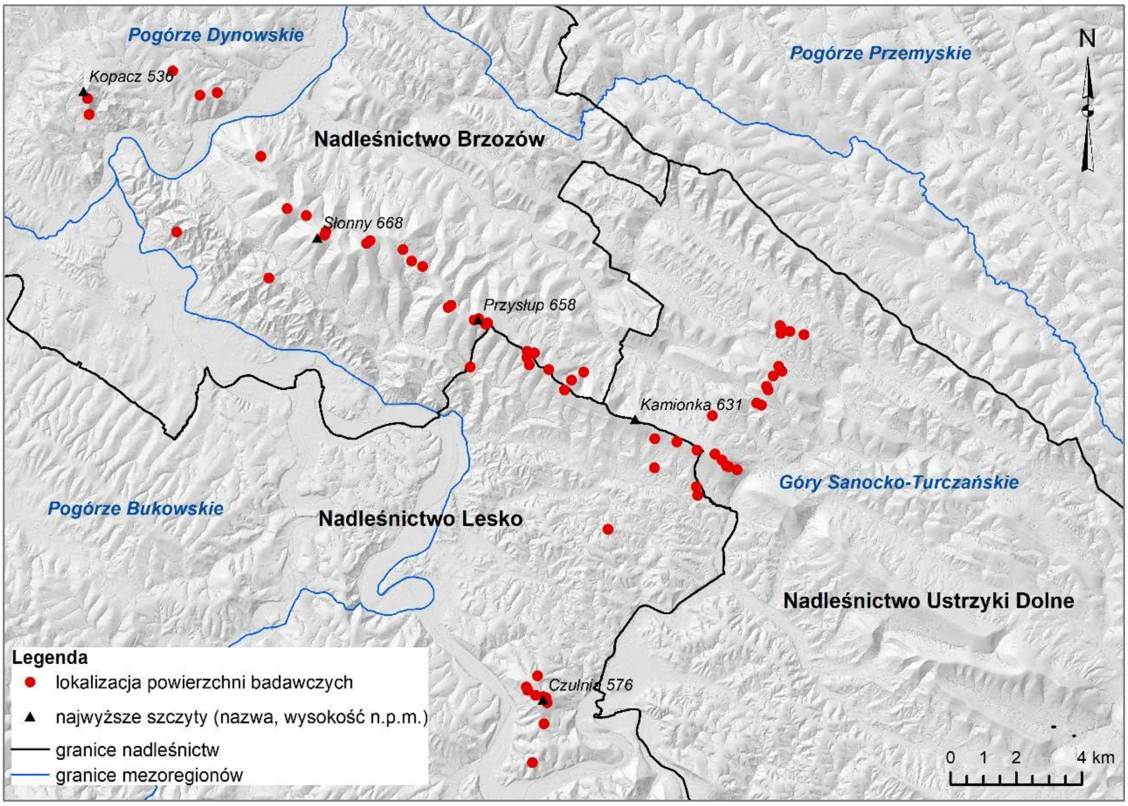
(1) długoterminowe zmiany zachodzące w roślinności warstwy zielnej lasów bukowych w polskich Karpatach Wschodnich zależne są od stadium rozwoju drzewostanu oraz prowadzonej gospodarki leśnej;

(2) kompozycja gatunkowa i różnorodność roślinności zielnej zmienia się wraz ze stadium rozwojowym drzewostanu;

(3) ważną rolę w długoterminowych zmianach kompozycji gatunkowej i różnorodności roślinności warstwy zielnej mogą odgrywać procesy o charakterze cyklicznym.

6. OPIS TERENU BADAŃ

Powierzchnie badawcze zostały zlokalizowane w Górach Sanocko-Turczańskich oraz będącym ich naturalnym przedłużeniem niewielkim fragmencie Pogórza Dynowskiego, w polskiej części Karpat Wschodnich. Dominującym zbiorowiskiem leśnym jest żyzna buczyna karpacka (*Dentario glandulosae Fagetum* Klika 1927 em. Mat. 1964), występująca na glebach brunatnych wykształconych z fliszu karpackiego (Dzwonko 1977; Skiba i Drewnik 2003). Lasy w których zostały założone powierzchnie badawcze służące do długoterminowych badań nad roślinnością znajdują się w zarządzie Nadleśnictwa Brzozów, Lesko i Ustrzyki Dolne. Ponad 90% drzewostanów w tym rejonie pełni funkcje ochronne. Teren ten wchodzi w skład sieci Natura 2000 - obszar Ostoja Góry Słonne PLH180013 oraz Góry Słonne PLB180003 (Ryc. 1).



Ryc. 1. Lokalizacja powierzchni badawczych

W latach 90. ubiegłego wieku został zmieniony sposób zagospodarowania polskich wschodnio karpackich lasów. Stosowaną wcześniej rębnie częściową prowadzącą do wykreowania drzewostanów jednopiętrowych i jednowiekowych (przy okresie odnowienia do 20 lat) zamieniono na rębnię stopniową, która ma na celu utworzenie drzewostanów wielopiętrowych i wielowiekowych podczas dłuższego okresu odnowienia wynoszącego 30-50 lat.

7. METODYKA

7.1. Zbieranie danych

Aby dowiedzieć się jakie zmiany zaszły na przestrzeni ponad 40 lat w roślinności lasów bukowych wykorzystano dane zebrane w trzech punktach czasowych na 67 półtrwałych powierzchniach badawczych wyznaczonych na podstawie niepublikowanych map i opisów ich lokalizacji wykonanych przez Profesora Z. Dzwonko (Dzwonko 1977). Pierwszy opis roślinności został wykonany w latach 1972-1973 (zwany dalej 1970.) (Dzwonko 1977). Druga inwentaryzacja roślinności miała miejsce w latach 2005-2007 (zwana dalej 2000.). Podczas drugiego okresu badawczego, wybrane do badań powierzchnie zostały ponownie zlokalizowane i oznaczone współrzędnymi geograficznymi (Durak i Holeksa 2015). Współrzędne geograficzne oraz weryfikacja lokalizacji powierzchni badawczych na podstawie opisów z lat 1970. i 2000. pozwoliły na dokładne odtworzenie ich lokalizacji podczas trzeciego okresu badań (w latach 2017-2018, zwanego dalej 2010.) (Ryc. 2).

Badania w latach 2010. prowadzono od maja do lipca. Aby zapewnić porównywalność danych, spisy roślinności wykonano na poletkach o tej samej powierzchni (od 200 do 400 m^2) i w podobnych terminach jak w przeszłości. W trzecim okresie badawczym, oprócz zdjęć fitosocjologicznych wykonanych na 67 półtrwałych powierzchniach badawczych prowadzono badania na dodatkowych powierzchniach o stałej wielkości 300 m^2 i zlokalizowanych w miejscach istniejących już powierzchni badawczych. Na dodatkowych powierzchniach zmierzono parametry drzewostanu takie jak: liczba drzew, pierśnica (wszystkich drzew o średnicy ≥ 7 cm mierzona na wysokości 1,3 m nad poziomem gruntu) oraz wysokość drzew (zmierzono wysokości drzewa o pierśnicy zbliżonej do przeciętnej w danej grupie wiekowej, a w przypadku znacznego zróżnicowania na grupy grubości pomiar 1-2 drzew w grupach grubości 7-20 cm, 20-40 cm, powyżej 40 cm). Zmierzono również masę ściółki i objętość martwego drewna na każdej powierzchni badawczej. Pomiarowi podlegało martwe drewno, które w grubszym końcu miało średnice większą niż 5 cm, a długość większą niż 0,5 m oraz pniaki, dla których zapisano ich wysokość i średnice. Próbki ściółki pobrano w 5 punktach (używając ramki o powierzchni 225 cm^2) znajdujących się na każdym rogu powierzchni badawczej oraz w jej części centralnej.

Dla wydzieleń leśnych w który zlokalizowano powierzchnie badawcze zebrano dane z inwentaryzacji drzewostanów (tzw. opisów taksacyjnych) znajdujących się w Planach

Urządzenia Lasu wg stanu na rok: 1976 - Nadleśnictwo Brzozów i Lesko; 1977 - Nadleśnictwo Ustrzyki Dolne; 2007 - Nadleśnictwo Brzozów; 2009 - Nadleśnictwo Lesko i Ustrzyki Dolne; 2017 - Nadleśnictwo Brzozów; 2019 - Nadleśnictwo Lesko i Ustrzyki Dolne. Był to: wskaźnik zadrzewienia, średnia pierśnica gatunku dominującego, średnia wysokość gatunku dominującego, zasobność, udział pokrycia warstwy podrostu, średnia wysokość gatunku dominującego w podroście, udział pokrycia warstwy nalotu, udział pokrycia warstwy podszytu, klasa wieku gatunku dominującego, średni wiek gatunku dominującego. Ważną informacją był również sposób zagospodarowania lasu (rodzaj rębni lub cięć pielęgnacyjnych) w danym wydzieleniu leśnym.

Ryc. 2. Drzewostan w stadium terminalnym w którym znajdowała się powierzchnia badawcza (lata 2010.)

Do przeanalizowania struktury wiekowej i gatunkowej drzewostanów znajdujących się w zasięgu wymienionych wyżej nadleśnictw wykorzystano dane z tabel powierzchniowych klas wieku według gatunków panujących znajdujących się w Planach Urządzenia Lasu.

W celu określenia zmian lesistości na badanym terenie, pozyskano dane przestrzenne opracowane w ramach projektu FORECOM tj. mapy rozmieszczenia lasów w Karpatach Polskich w latach 1860., oraz 1930. i 1970. (Kozak i Szwagrzyk 2016). Lesistość dla lat 2000. i 2010. określono na podstawie danych z projektu CORINE Land Cover (Chief

Inspectorate of Environmental Protection, https://clc.gios.gov.pl) gdzie podstawą wykreślenia poszczególnych form użytkowania ziemi były zdjęcia satelitarne.

Aby sprawdzić zmiany warunków klimatycznych wykorzystano dane meteorologiczne udostępnione przez Instytut Meteorologii i Gospodarki Wodnej - Państwowy Instytut Badawczy (https://meteomodel.pl) dla stacji Lesko (420 m n.p.m.) z lat 1966-2018.

7.2. Analiza danych

Przemiany w zbiorowiskach roślin zielnych lasów bukowych rozpatrywano na podstawie danych florystycznych ze zdjęć fitosocjologicznych z lat 1970., 2000. i 2010. W analizie wykorzystano pokrycie warstwy drzew i krzewów, całkowite pokrycie warstwy drzew i krzewów (Ewald i in. 2011), pokrycie roślinności zielnej, liczbę gatunków: drzew, krzewów, siewek drzew, roślin zielnych na powierzchniach badawczych. Wyróżniono i porównano ekologiczne grupy gatunków obejmujące: gatunki o niskich i wysokich wymaganiach siedliskowych (na podstawie liczb wskaźnikowych Ellenberga (1992)), gatunki starych lasów (wg. Hermy i in.1999.; Dzwonko i Loster 2001), gatunki diagnostyczne dla lasów bukowych, gatunki diagnostyczne zbiorowisk porębowych ze związku *Atropetalia* i klasy *Epilobietea angustifolii* (zgodnie z nomenklaturą fitosocjologiczną wg. Matuszkiewicza (2001)). Dla każdego zdjęcia fitosocjologicznego obliczono liczbę gatunków reprezentujących grupę gatunków szybko oraz wolno rozprzestrzeniających się (Hermy i in. 1999; Dzwonko i Loster 2001). Do gatunków szybko rozprzestrzeniających się zaliczono anemochory, endozoochory, epizoochory. Do grupy gatunków wolno rozprzestrzeniających się zaliczono: myrmekochory, hydrochory, baro- i autochory (Hermy i in. 1999; Dzwonko i Loster 2001). Zidentyfikowano gatunki zwycięskie i przegrane do których zaliczono tylko te których frekwencja występowania między pierwszym i drugim lub drugim i trzecim okresem badań wzrosła lub zmniejszyła się o co najmniej 10% lub liczebność między trzema spisami roślinności wykazała znaczny wzrost lub spadek.

Aby określić warunki siedliskowe panujące na powierzchniach badawczych wykorzystano wartości wskaźników Ellenberga (Ellenberg i in. 1992) dla światła (L), temperatury (T), wilgotności gleby (F), odczynu gleby (R) i azotu zawartego w glebie (N) na podstawie udziału jakościowego tj. występowania gatunku w zdjęciu fitosocjologicznym. Użyte wskaźniki pozwalają na pośrednie określenie zmian warunków siedliskowych (Diekmann 2003). W analizach uwzględniających udział ilościowy poszczególnych gatunków, stopnie ilościowości Braun-Blanqueta zamieniono na przeciętny procent pokrycia (Pawłowski 1977).

Do analiz różnorodności alfa i beta wykorzystano wskaźnik Shannona, Sorensa i Simpsona (Baselga 2010). Różnorodność gamma została zdefiniowana jako całkowita pula gatunków odnotowana w danym spisie. Do wykrycia biotycznej homogenizacji lub zróżnicowania roślinności zielnej przyjęto metodę opartą na średnich niepodobieństwach między powierzchniami badawczymi (Van Calster i in. 2007; Rooney i in. 2004, Durak i in. 2015; Olden i Poff 2003). Dla uzyskania pełniejszej odpowiedzi na temat stanu zachowania roślinności zielnej, analizowano różnorodność alfa wyróżnionych ekologicznych grup gatunków. Analizy zróżnicowania roślinności zielnej przeprowadzono na tle zmian w strukturze drzewostanów (zobrazowanych za pomocą stadiów rozwojowych) oraz zmian w gospodarce leśnej.

Do oszacowania intensywności użytkowania lasu wykorzystano informacje na temat działań gospodarczych prowadzonych w poszczególnych okresach badawczych wg. Planów Urządzenia Lasu. Działania gospodarcze uszeregowano w pięciostopniowej skali od najmniej do najbardziej inwazyjnych a następnie przypisano do każdego zdjęcia fitosocjologicznego i oceniono zmiany między okresami badawczymi.

Aby porównać strategie życiowe dominujące w zbiorowiskach roślin zielnych, zastosowano model C-S-R (Grime 1977, 2001). W tym celu obliczono średni udział strategii C, S i R dla każdego ze zdjęć fitosocjologicznych z trzech okresów badawczych korzystając z klasyfikacji gatunków zaproponowanej przez Pierce i in. (2017). Dla lepszego zrozumienia zmian w roślinności zielnej, zarówno dla poszczególnych okresów badawczych jak i etapów rozwojowych lasu, zidentyfikowano specyficzne dla nich zestawy gatunków za pomocą analizy gatunków wskaźnikowych (Dufrene i Legendre 1997).

W analizach ujęto wszystkie gatunki z wyjątkiem geofitów wczesnowiosennych (tych które kwitną od lutego do kwietnia i mają krótkotrwałe pędy naziemne np. *Adoxa moschatellina* czy *Galanthus nivalis*). W celu uniknięcia błędów wynikających z nieprawidłowej identyfikacji podobnych gatunków paproci z rodzaju *Dryopteris* połączono je w jedną grupę. Tak samo postąpiono z gatunkiem *Senecio fuchsii* i *S. nemorensis*.

Do identyfikacji stadiów rozwojowych drzewostanów, w których znajdowały się powierzchnie badawcze w poszczególnych okresach badawczych, opracowano metodę wykorzystując dane zebrane na 300 m^2 powierzchniach badawczych w latach 2017-2018 oraz dane zawarte w Planach Urządzenia Lasu (Durak i in. 2021). Metoda ta pozwala określić stadia rozwoju drzewostanu na podstawie 10 archiwalnych zmiennych drzewostanowych (pochodzących z Planów Urządzenia Lasu i zdjęć fitosocjologicznych): wskaźnika zadrzewienia, średniej pierśnicy gatunku dominującego, średniej wysokości gatunku dominującego, zasobności drzewostanu, klasy wieku według gatunku dominującego, średniego wieku gatunku dominującego, sumarycznego pokrycia warstwy drzew i krzewów, pokrycia warstwy drzew, pokrycia warstwy krzewów i średniej wysokości drzew.

Klasy wieku przypisano na podstawie wieku gatunku dominującego stosując dwudziestoletnie przedziały (I:1-20; II: 21-40; III: 41-60; IV: 61-80; V: 81-100; VI: 101-120; VII i starsze więcej niż 121 lat). Jako RP (*regeneration period*) oznaczono drzewostany będące w klasie odnowienia i klasie do odnowienia tj. takie w których prowadzone jest użytkowanie rębne.

Średnie temperatury i średnią sumę opadów obliczono dla okresów dziesięcioletnich (1966-1975; 1999-2008; 2009-2018). Wybór zakresu lat nawiązuje do dziesięcioletnich okresów obowiązywania Planów Urządzenia Lasu w trakcie których wykonywane były badania na powierzchniach badawczych. Do porównań wykorzystano dane klimatyczne dla miesięcy z okresu wegetacyjnego tj. od kwietnia do sierpnia, podobnie jak to zrobili Bosela i in. 2016 oraz Thom i in. 2020.

Testem ANOVA lub Friedmana w zależności od spełnienia założenia o normalności rozkładu badano różnice w: strukturze lasu, intensywności użytkowania, pokryciu poszczególnych warstw, frekwencji gatunków, bogactwie gatunkowym, różnorodności gatunków, liczbie gatunków w wyróżnionych grupach ekologicznych, strategii życiowej roślinności pomiędzy okresami badawczymi. Do zbadania różnicy w powyższych zmiennych pomiędzy stadiami rozwojowymi drzewostanów użyto testu ANOVA lub Kruskala–Wallisa. W celu ujawnienia zależności między zmianami struktury drzewostanu, intensywnością gospodarki leśnej oraz wskaźnikami różnorodności zastosowano test korelacji rang Spearmana. Porównanie cech drzewostanu w poszczególnych stadiach rozwojowych wykonano przy użyciu liniowej analizy dyskryminacji LDA. Do przedstawienia zmian w składzie warstwy zielnej pomiędzy stadiami rozwojowymi drzewostanu i okresami badań zastosowano niemetryczne skalowanie wielowymiarowe NMDS. W celu wyjaśnienia zmian w kompozycji gatunkowej warstwy zielnej współrzędne I i II osi NMDS skorelowano z analizowanymi cechami warstwy zielnej i zmiennymi drzewostanowymi za pomocą testu korelacji rang

Spearmana. W celu potwierdzenia różnicy w kompozycji gatunkowej roślinności zielnej między fazami rozwojowymi i okresami badawczymi wykonano wielowymiarową, nieparametryczną analizę wariancji PerMANOVA.

Analizy statystyczne wykonano przy użyciu pakietu oprogramowania PAST (Hammer i in. 2001) oraz STATISTICA (StatSoft Inc.). Analizę lesistości w poszczególnych okresach wykonano przy użyciu programu ArcMap 10.7 (ESRI, Redlands, CA, USA). Dane wektorowe z lat 1860., 1930., 1970., 2000. i 2010. przycięto do terenu badań, a następnie obliczono powierzchnię lasów i lesistość w kolejnych okresach.

8. WYNIKI

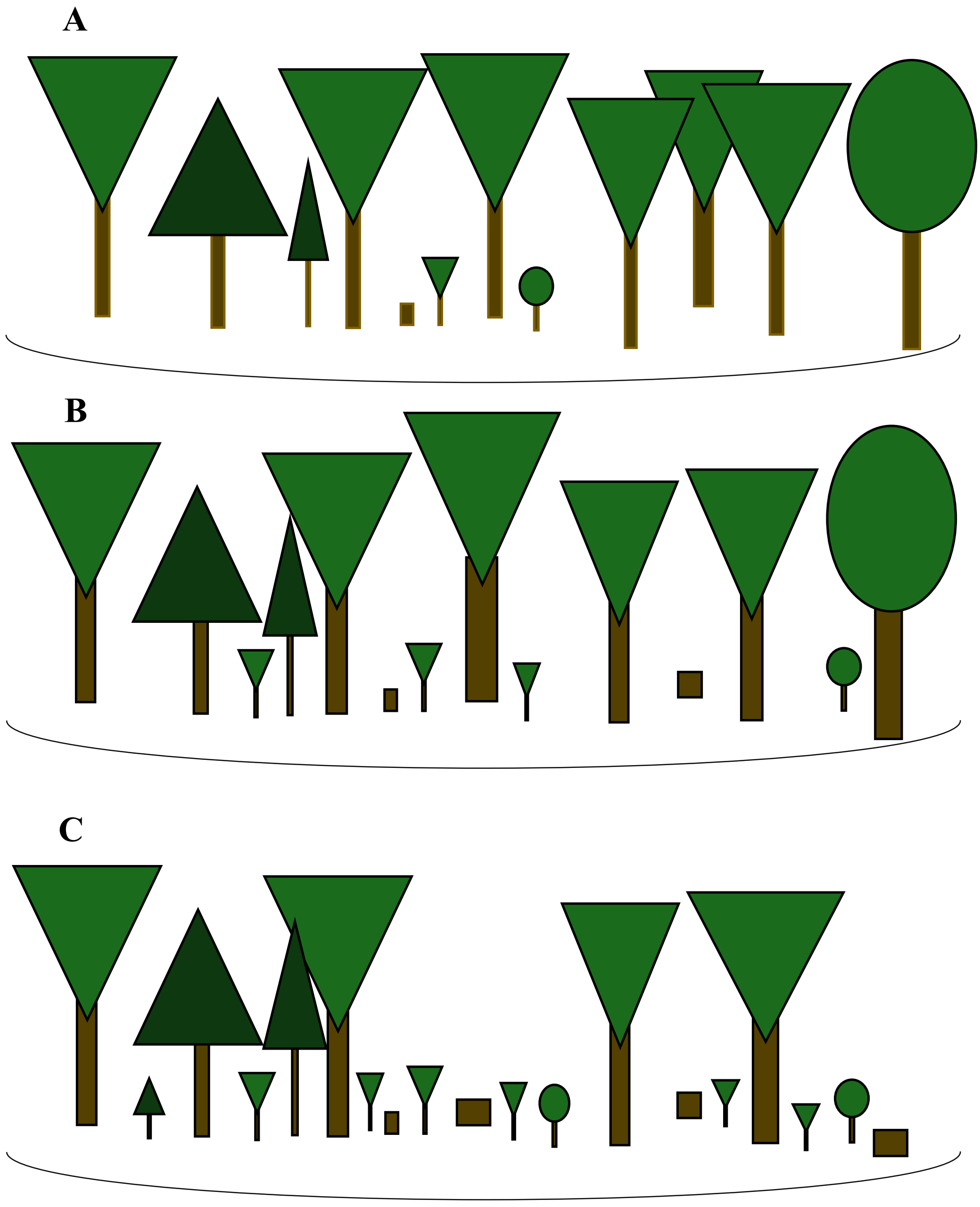
8.1. ZMIANY W ROŚLINNOŚCI ZIELNEJ, STRUKTURZE LASU I GOSPODARCE LEŚNEJ ORAZ WARUNKACH KLIMATYCZNYCH MIĘDZY OKRESAMI BADAWCZYMI

8.1.1. ZMIANY W STRUKTURZE DRZEWOSTANÓW, GOSPODARCE LEŚNEJ I LESISTOŚCI

Powierzchnia lasów w zasięgu administracyjnym Nadleśnictwa Brzozów, Lesko i Ustrzyki Dolne od roku 1860 do 2010. wzrosła blisko dwukrotnie. Największy przyrost powierzchni leśnej nastąpił pomiędzy 1930. i 1970. W tym okresie wzrosła ona z 26,1% do 42,8%, co było głównie efektem wyludnienia tych terenów. W kolejnych latach powierzchnia lasów nadal rosła, ale o wiele wolniej, osiągając poziom 47,6% w 2010. (**Publikacja 2**: Rycina 2).

Struktura wiekowa drzewostanów rosnących na terenie badań według gatunków panujących od 1970. do 2010. roku znacząco się zmieniła. W 1970. dominowały drzewostany w drugiej klasie wieku (21-40 lat) - 32,6%. W 2000. największy udział przypadał na klasę trzecią (41-60 lat), a następnie na drzewostany będące w okresie odnowienia (KO i KDO, w publikacjach oznaczone jako RP - *regeneration period*) - 27,3%. W latach 2000. i 2010. największy udział powierzchniowy stanowiły drzewostany będące w trakcie odnawiania (27,3% i 28,6%) (**Publikacja 2**: Rycina 3).

Dane dotyczące powierzchni badawczych potwierdzają obserwowany na całym terenie badań wzrost wieku drzewostanów. Stwierdzono również, że w kolejnych okresach badawczych malało zwarcie warstwy drzew, a rosło zwarcie warstwy krzewów; jednak dopiero w latach 2010. zmiany te były istotne statystycznie. Spadek zwarcia warstwy drzew, a także ich wysokości, w połączeniu ze wzrostem zwarcia warstwy krzewów świadczą o intensyfikacji pozyskania drzew w wieku rębności i nasileniu procesów związanych z odnowieniem lasu. (**Publikacja 1**: Tabela 2, Rycina 3) (Ryc.3)



Ryc. 3. Struktura drzewostanów w okresach badawczych: A - 1970., B - 2000., C - 2010.

Dane z inwentaryzacji drzewostanów wskazują na to, że pomiędzy latami 1970. a 2010. na terenie Nadleśnictwa Brzozów, Lesko i Ustrzyki Dolne zwiększył się udział drzewostanów, w których gatunkiem dominującym był buk (z 27,6% do 34,1%). Wyniki te potwierdzają się w danych dotyczących powierzchni badawczych, gdzie pokrycie procentowe buka pomiędzy pierwszym a trzecim okresem wrosło średnio z 47,4% do 54,9%. Pomiędzy 2000. a 2010. zmieniło się również średnie pokrycie procentowe gatunków domieszkowych (wzrosło dla jodły z 10,4% do 14,1%, a zmalało dla jawora z 8,6% do 7,3% i jesionu z 2,7% do 0,1% (**Publikacja 2**: Tabela 1,2).

Pomiędzy latami 1970. a 2000. zaobserwowano istotne zmiany w intensywności gospodarki leśnej. W latach 1970. ponad 45% powierzchni próbnych znajdowało się drzewostanach, w których presja gospodarki leśnej była niewielka (cięcia pielęgnacyjne - trzebieże), jednocześnie niemal drugie tyle powierzchni znalazło się w miejscach, gdzie działania gospodarcze prowadzone były intensywnie (rębnie częściowe). W latach 2000. presja gospodarki leśnej spadła wraz ze zmianą sposobu zagospodarowania (rębnie częściowe zastąpiono rębniami stopniowymi). W latach 2010. większość drzewostanów osiągnęła wiek rębności, przez co zmniejszyła się liczba powierzchni badawczych w obrębie których działania gospodarcze były prowadzone na mniejszą skalę; intensywność gospodarki leśnej wzrosła (**Publikacja 1**: Tabela 2, Rycina 2, 3).

8.1.2. ZMIANA WARUNKÓW KLIMATYCZNYCH

Średnia temperatura okresu wegetacyjnego (tj. miesięcy od kwietnia do sierpnia) między okresami badawczymi stopniowo rosła: 1970.: 13,7°C, 2000.: 14,6°C, 2010.: 15,1°C. Średni wzrost temperatury okresu wegetacyjnego pomiędzy 1970. a 2010. wyniósł 1,4°C. W przypadku średniej sumy opadów okresu wegetacyjnego zaobserwowano, że wartość odnotowana w latach 2010. była wyraźnie mniejsza (463,8 mm) od średniej wartości w latach 1970. (516,3 mm) i 2000. (513,7 mm) (**Publikacja 2**: Rycina 5 i 6).

8.1.3. ZMIANY W KOMPOZYCJI GATUNKOWEJ ROŚLINNOŚCI ZIELNEJ

Na poziomie zbiorowiska średnia frekwencja występowania gatunków była najwyższa w latach 2000., na średnim poziomie kształtowała się w latach 1970., a na najniższym w latach 2010. Podobne dane otrzymano analizując średnie bogactwo gatunkowe na poziomie powierzchni badawczej. Wyniki statystyczne wskazują na spadek bogactwa gatunkowego i wzrost ogólnej liczebności gatunków w latach 2010 (**Publikacja 1**: Tabela 3).

W 2010. odnotowano mniejsze średnie pokrycie warstwy zielnej oraz mniejszą średnią liczbę gatunków roślin zielnych na powierzchniach badawczych niż w poprzednich okresach. Również średnia liczba gatunków starych lasów oraz gatunków wskaźnikowych dla żyznej buczyny karpackiej istotnie spadła w porównaniu do lat 1970. i 2000. Liczba gatunków porębowych na przestrzeni lat nie zmieniła, jednak istotnie wzrosło ich pokrycie. Ponadto w latach 2010. było mniej gatunków: o małych wymaganiach świetlnych i termicznych, wymagających wilgotnych gleb o niskim pH i dużej zawartości substancji odżywczych. Wśród roślin zielnych w okresie badań 2010. odnotowano mniejszy udział gatunków o strategii życiowej C, oraz większy udział gatunków o strategii S (**Publikacja 2**: Tabela 3, Rycina 4; **Publikacja 3**: Tabela 1).

W gronie 20 gatunków które można nazwać „zwycięzcami" na podstawie trzech okresów badawczych, największy wzrost odnotowały te których występowanie związane jest ze zmianami w drzewostanach, a także mające wyższe wymagania świetlne (*Rubus hirtus* oraz paprocie z rodzaju *Dryopteris*). Liczba „przegranych" była o wiele wyższa - 45 gatunków. Z pośród nich największy spadek dotyczył gatunków cienioznośnych, typowych dla żyznych buczyn (*Actaea spicata*, *Athyrium filix-femina*, *Daphne mezereum*, *Mercurialis perennis*, *Oxalis acetosella* i *Polygonatum multiflorum*). W grupie przegranych znalazły się też gatunki diagnostyczne dla żyznej buczyny karpackiej: *Dentaria glandulosa*, *D. bulbifera*, *Symphytum cordatum*, *S. tuberosum*, *Euphorbia amygdaloides* i *Glechoma hirsuta*. Dodatkowo znaleziono grupę gatunków, których częstotliwość występowania zmniejszyła się, a liczebność wzrosła w pomiędzy latami 1970. i 2010. np. *Galeobdolon luteum* i *Fagus sylvatica* (**Publikacja 1**: Tabela S1).

8.1.4. ZMIANY RÓŻNORODNOŚCI ROŚLINNOŚCI ZIELNEJ

Największą różnorodność gamma odnotowano w 2010. (131 gatunków), podczas gdy w 1970. i 2010. była ona podobna (117 i 118 gatunków). Różnorodność alfa, wyrażona wskaźnikiem różnorodności Shannona była największa w 2000. a najmniejsza w 2010. Beta różnorodność wyrażona współczynnikiem podobieństw Sorensena i wskaźnikiem Simpsona była największa w 2010. a najmniejsza w 2000. W ciągu ponad 40 lat wzrosła heterogeniczność siedlisk leśnych pomiędzy powierzchniami badawczymi (**Publikacja 1**: Tabela 3, Rycina 4).

Między latami 2000. i 2010. w porównaniu do 1970. i 2000. wskaźniki różnorodności alfa wykazał spadek, który był ujemnie skorelowany ze wzrostem pokrycia warstwy krzewów. Również pomiędzy latami 2000. i 2010. różnorodność beta zanotowała wzrost, który był skorelowany ujemnie ze spadkiem wysokości drzew i liczbą gatunków drzew. (**Publikacja 1**: Tabela 3).

Różnorodność alfa (wyrażona za pomocą bogactwa gatunkowego) ekologicznych grup gatunków, w przypadku gatunków o wysokich lub niskich wymaganiach siedliskowych, w latach 2000. była najwyższa dla wszystkich grup. W latach 2010. Istotnie mniejsza była liczba gatunków w grupach L_L, T_L, F_H, R_H i N_H (**Publikacja 1**: Tabela 3).

8.2. ZMIANY ROŚLINNOŚCI ZIELNEJ MIĘDZY STADIAMI ROZWOJOWYMI LASU

8.2.1. CHARAKTERYSTYKA STADIÓW ROZWOJOWYCH I ICH DYNAMIKA

W oparciu o metodę zaproponowaną przez Duraka i in. (2021) w każdym okresie badawczym wyróżniono i scharakteryzowano trzy szeroko ujęte stadia rozwojowe drzewostanu: dorastania, optymalne i terminalne. Z pośród danych z inwentaryzacji drzewostanów (wykonywanych na potrzeby planów urządzenia lasu) stadia rozwojowe najlepiej wyróżniały takie zmienne jak: wskaźnik zadrzewienia, średnia wysokość, średnia pierśnica drzew, a także średni wiek i klasa wieku (na podstawie gatunku głównego). Biorąc pod uwagę dane zanotowane na powierzchniach badawczych stadia rozwojowe drzewostanu różniły się pod względem pokrycia warstwy drzew, pokrycia warstwy krzewów oraz łącznego pokrycia drzew i krzewów (**Publikacja 3**: Tabela 3).

Stadium dorastania charakteryzowało się wysokim wskaźnikiem zadrzewienia, niskim wiekiem, niską wysokością i pierśnica drzew. W stadium optymalnym zasobność drzewostanu była największa, a wiek, wysokość i pierśnica miały wartości pośrednia pomiędzy stadium dorastania a terminalnym. W stadium terminalnym wskaźnik zadrzewienia był najmniejszy, podobnie jak pokrycie warstwy drzew. Największe wartości odnotowano dla pierśnicy i wieku drzewostanu (**Publikacja 3**: Tabela 3, A2).

Pomimo, że w każdym okresie badawczym wyodrębniono stadium dorastania, optymalne i terminalne, to liczba reprezentujących je powierzchni zmieniała się w czasie. W pierwszym okresie badań (lata 1970.) dobrze reprezentowane było stadium dorastania i optymalne (odpowiednio 22 i 40 powierzchni badawczych). W latach 2000. Drzewostany większości powierzchni reprezentujących wcześniej stadium dorastania przeszły do wyraźnie dominującego w tym okresie stadium optymalnego (łącznie 47 powierzchni). W 2010. duża część powierzchni, które wcześniej reprezentowały stadium optymalne, znalazła się w stadium terminalnym (łącznie 36 powierzchni). W efekcie liczba powierzchni badawczych, których drzewostany reprezentowały stadium optymalne zmniejszyła się prawie o połowę, a w przypadku stadium dorastania prawie całkowicie znikła (**Publikacja 3**: Tabela 3, Rycina 3).

8.2.2. ZMIANY W KOMPOZYCJI GATUNKOWEJ ROŚLINNOŚCI ZIELNEJ

Statystyczna analiza NMDS oraz PerMANOVA wykazały istnienie różnic pomiędzy kompozycją gatunkową roślinności runa między poszczególnymi stadiami rozwojowymi drzewostanów. Korelacja między osiami analizy NMDS, a cechami drzewostanu i warstwy zielnej ujawniła pewne gradienty zmiany składu gatunkowego warstwy zielnej między stadiami. Pierwsza oś NMDS była dodatnio skorelowana z wiekiem drzewostanu i pierśnicą, a także z liczbą gatunków o wysokich wymaganiach co do wilgotności, zasobności w azot i kwasowości gleby. Korelacja ujemna wystąpiła z liczbą gatunków o wysokich wymaganiach termicznych oraz liczbą gatunków o niskich wymaganiach odnoście kwasowości i żyzności gleby. Wzdłuż pierwszej osi NMDS zauważono wzrost liczby gatunków diagnostycznych dla żyznej buczyny karpackiej oraz tych o strategii życiowej C oraz spadek gatunków o strategii S. Druga oś NMDS była silnie dodatnio skorelowana ze zmianą czasu między okresami badawczymi oraz takimi zmiennymi jak pierśnica, wysokość drzew, pokrycie warstwy krzewów i wiek drzewostanu. Ponadto oś ta była dodatnio skorelowana z liczbą gatunków o wysokich wymaganiach świetlnych (**Publikacja 3**: Tabela 1, A1, Rycina 4).

Wraz ze zmianą stadiów rozwojowych drzewostanu zmieniała się kompozycja gatunkowa roślin zielnych. Gatunki stadium dorastania miały niskie wymagania co do ilości światła i azotu w glebie (np. *Lathyrus vernus*, *Luzula pilosa* i *Polygonatum multiflorum*). Przeważały te o strategii życiowej R (średnio ponad 55%) oraz C (średnio 40%). Wymagania siedliskowe gatunków ze stadium optymalnego były wyższe. Centrum występowania miały w nim gatunki starych lasów i te wymagające przeciętnych warunków świetlnych oraz średnio zasobnych gleb (np. *Actaea spicata*, *Dentaria bulbifera*, *Lunaria rediviva*, *Pulmonaria obscura* i *Stellaria nemorum*). W strategii życiowej roślin dominowała strategia C i R, przy czym udział strategii C był najwyższy w porównaniu do innych stadiów. Kompozycja gatunkowa stadium terminalnego charakteryzowała się większym udziałem gatunków o zwiększonych wymaganiach odnośnie światła i zawartości azotu w glebie. Odnotowano większe pokrycie gatunków występujących w śródleśnych prześwietleniach (np. *Rubus hirtus*, *Senecio sp.*, *Stachys* *sylvatica*, *Urtica dioica* i *Rumex obtusifolius*). Wśród strategii życiowej roślin dominowała strategia C i R, jednak w porównaniu do stadium dorastania i optymalnego udział strategii C był mniejszy (**Publikacja 3**: Tabela A3, A4, Rycina 5).

8.2.3. ZMIANY W RÓŻNORODNOŚCI ROŚLINNOŚCI ZIELNEJ

W stadium optymalnym odnotowano najwyższą różnorodność alfa i najmniejszą różnorodność beta. Niska różnorodność beta wynikała z dużego podobieństwa pod względem składu gatunkowego pomiędzy powierzchniami badawczymi. Wynikało ono z niewielkiego poziomu zaburzeń i utrzymujących się warunków siedliskowych, optymalnych dla gatunków leśnych. W stadiach dorastania i terminalnym (różniącym się m.in. wskaźnikiem zadrzewienia i wiekiem drzewostanu) różnorodność beta była wysoka ze względu na małe podobieństwo składu gatunkowego pomiędzy powierzchniami badawczymi. Miał na to wpływ wysoki poziom zaburzeń i większe zróżnicowanie warunków siedliskowych, występujące zwłaszcza w stadium terminalnym na skutek procesów odnawiania lasu. (**Publikacja 3**: Tabela 3, Rycina 6).

8.3. CZASOWE ZMIANY W KOMPOZYCJI GATUNKOWEJ I RÓŻNORODNOŚCI ROŚLINNOŚCI ZIELNEJ W KONTEKŚCIE STADIÓW ROZWOJOWYCH

8.3.1. WPŁYW STADIÓW ROZWOJOWYCH NA DŁUGOTERMINOWE ZMIANY W KOMPOZYCJI GATUNKOWEJ I RÓŻNORODNOŚCI ROŚLINNOŚCI ZIELNEJ

Statystyczne analizy NMDS wykazały kierunkowe zmiany kompozycji gatunkowej warstwy zielnej wzdłuż drugiej osi NMDS pomiędzy kolejnymi okresami badawczymi jak również kolejnymi stadiami rozwojowymi, co sugeruje duży wpływ stadium rozwojowego drzewostanu na zachodzące w roślinności runa zmiany w czasie. Zależność tą potwierdza dominacja kolejnych stadiów rozwojowych (optymalnego i terminalnego) w kolejnych okresach badawczych (latach 1970., 2000. i 2010.) oraz duże podobieństwo między cechami roślinności zielnej stadiów rozwojowych i zdominowanych przez nie okresów badawczych. Na przykład w latach 2000., podobnie jak w dominującym w tym okresie stadium optymalnym odnotowano większą liczbę: gatunków na powierzchniach badawczych, gatunków starych lasów, gatunków wolno rozprzestrzeniających się, tych z niskimi wymaganiami świetlnymi, oraz o wysokich wymaganiach troficznych, w porównaniu do 1970. czy 2010. Natomiast w latach 2010. podobnie jak w dominującym w tym okresie stadium terminalnym liczba gatunków na powierzchniach badawczych była najmniejsza w porównaniu do badań z lat 1970. czy 2010. Natomiast sumaryczne pokrycie gatunków zbiorowisk porębowych było największe (**Publikacja 3**: Tabela 1, Rycina 4).

Największą różnorodność alfa i najmniejszą różnorodność beta odnotowano w stadium optymalnym (dominującym w latach 2000). Niska różnorodność beta wynikała z dużego podobieństwa składu gatunkowego pomiędzy powierzchniami badawczymi. W stadium dorastania i terminalnym beta różnorodność była wysoka (głównie w stadium terminalnym w latach 2010). Wyniki wskazują na homogenizację warstwy zielnej w stadium optymalnym (**Publikacja 3**: Tabela 1, Rycina 6).

9. DYSKUSJA

9.1. ZMIANY W KOMPOZYCJI GATUNKOWEJ I RÓŻNORODNOŚCI ROŚLINNOŚCI MIĘDZY OKRESAMI BADAWCZYMI

9.1.1. ZMIANY W STRUKTURZE DRZEWOSTANÓW, GOSPODARCE LEŚNEJ, LESISTOŚCI ORAZ WARUNKÓW KLIMATYCZNYCH I ICH WPŁYW NA KOMPOZYCJĘ GATUNKOWĄ ROŚLINNOŚCI ZIELNEJ

Z przedstawionych danych wynika, że lesistość w obecnym zasięgu administracyjnym Nadleśnictwa Brzozów, Lesko i Ustrzyki Dolne od lat 1860. do 2010. wzrosła z 25,2% do 47,6% i jest dużo wyższa niż przeciętna lesistość w Polsce, która wynosi 29,6% (Rozkrut 2020). Zmiany lesistości na badanym terenie w dużym stopniu odpowiadają zmianom obserwowanym w polskich Karpatach, gdzie od połowy XIX wieku do 2010. lesistość wzrosła z 27% do 47% (Kozak 2010; Kozak i Szwagrzyk 2016). Spowodowało to powstanie rozległych kompleksów leśnych przyczyniając się do zmniejszenia fragmentacji lasów, zwłaszcza w południowej i południowo-wschodniej części polskich Karpat (Kozak i in. 2018). Zmniejszenie fragmentacji lasów jest jednym z czynników ograniczających zanikanie leśnych gatunków roślin zielnych (Matlack i Monde 2004; Matlack 2005). Przeprowadzona analiza zmian w warstwie roślin zielnych wykazała w latach 2000. większą liczbę gatunków wolno rozprzestrzeniających się oraz gatunków starych lasów niż w latach 1970. Natomiast w latach 2010. mimo zaobserwowano spadek liczby gatunków typowych dla lasów bukowych i wolno rozprzestrzeniających się. W lasach gospodarczych na kompozycję gatunkową runa wpływają również działania techniczne (przejazdy, naruszenie gleby itd.) wykonywane podczas ścinki drzew (Bergstedt i in. 2008). W badanych lasach z lat 2010. to właśnie intensywności działań gospodarczych związanych z zaawansowaną rębnią z jednej strony oraz wzrost zwarcia podszytu z drugiej strony mogły przełożyć się na ogólny spadek liczby gatunków roślin w warstwie zielnej.

Struktura drzewostanu wpływa na różnorodność gatunkową roślin zielnych, kształtuje warunki siedliskowe oraz mikroklimat (Jacob i in. 2009; Helmy i in. 2017; Ujházy i in. 2017). Pomiędzy okresami badań (lata 1970., 2000. i 2010.) struktura drzewostanów znacząco się zmieniła. Nastąpił wzrost udziału drzewostanów w VI klasie wieki i w klasie odnowienia oraz spadek udziału drzewostanów młodszych, będących w II i III klasie wieku. Podczas naturalnego starzenia się lasu bukowego maleje liczba gatunków domieszkowych (Mölder i in. 2014). W drzewostanach znajdujących się na terenie badań zauważono spadek udziału gatunków stanowiących cenną domieszkę tj. jawora i jesionu co mogło przyczynić się do zubożenia gleby w składniki odżywcze oraz jej zakwaszenia (Augusto i in. 2003; Langenbruch i in. 2012). Prawidłowość tą wydają się potwierdzać wyniki badań na powierzchniach badawczych. Wprawdzie nie stwierdzono spadku zawartości składników odżywczych (EIV N), ale jednak wykazano wzrost kwasowości gleby (EIV R) pomiędzy 1970. a 2010.

Dane z powierzchni badawczych wskazują również na sukcesywny spadek zwarcia warstwy drzew w kolejnych okresach badawczych: 1970. – 87,3%, 2000. – 84,0%, 2010. – 77,6%. Jednak powstające luki stosunkowo szybko wypełniane są przez podrost, którego końcowe zwarcie w latach 2010. osiągnęło średnio 27,2%. W efekcie stwierdzono tylko nieznaczny, nieistotny statystycznie spadek łącznego pokrycia warstwy drzew i krzewów pomiędzy trzema okresami badawczymi. Mimo to zmianie uległy warunki siedliskowe związane z warunkami świetlnymi na dnie lasu i wilgotnością gleby - wzrosła ilość dostępnego światła (EIV L) i zmniejszyła się wilgotność gleby (EIV F) w 2010. Wraz ze wzrostem wieku drzewostanu zwiększała się ilość światła docierającego do dna lasu w wyniku naturalnego obumierania drzew lub działań gospodarczych. Zwiększająca się ilość światła przyczyniła się do szybszego uwalniania składników pokarmowych z nagromadzonej materii organicznej na dnie lasu (Facelli i Pickett 1991). Roślinność zielna z lat 2000. charakteryzowała się znacznie większym udziałem gatunków mezotroficznych lasów liściastych niż w latach 1970. W latach 2010. na skutek większego prześwietlenia odnotowano większe pokrycie gatunków związanych ze śródleśnymi prześwietleniami, o większych wymaganiach świetlnych i troficznych.

Wyniki przeprowadzonych analiz różnic w roślinności zielnej stadiów rozwojowych lasu i okresów badawczych potwierdziły istotną rolę dostępności światła w kształtowaniu składu gatunkowego warstwy zielnej buczyny karpackiej. Depauw i in. (2019) doszli do podobnych wniosków, analizując lasy strefy umiarkowanej w całej Europie.

Zmiany klimatyczne bezpośrednio lub pośrednio wpływają na leśną roślinność zielną. Wpływ ten zwiększa się w przypadku przerzedzanie koron drzew skutkującego zwiększeniem temperatury na dnie lasu oraz spadkiem wilgotności gleby (Thom i in. 2020; Zellweger i in. 2020). Na przestrzeni ostatnich ponad 40 lat w sezonie wegetacyjnym wzrosła średnia temperatura oraz zmalała średnia suma opadów. W latach 2000., gdy dominująca część drzewostanów znajdowała się w stadium optymalnym, a intensywność działań gospodarczych była umiarkowana wpływ zmian klimatycznych mógł być buforowany przez zwartą warstwę koron drzew (Thom i in. 2020, Zellweger i in. 2020). W 2010. drzewostany te wkroczyły w stadium terminalne, wzrosła intensywność cięć rębnych, co w konsekwencji dało mniejsze pokrycie warstwy drzew i znacznie większe pokrycie podrostu.

Porównanie wskaźnika EIV T między okresami badań sugeruje jednak, że temperatura dna lasu nie uległa większej zmianie w latach 2010, co można przypisać buforującej roli rozwijającej się warstwy podrostu. Z drugiej strony, na negatywny wpływ ocieplenia klimatu może wskazywać stwierdzone zanikanie gatunków o niskich wymaganiach termicznych (**Publikacja 3**: Tabela 1). Spadek średniej sumy opadów w sezonie wegetacyjnym 2010. to druga obok zmian w strukturze drzewostanów ważna przyczyna zarejestrowanego w latach 2010. spadku wilgotności gleby (EIV F). Niższa wilgotność gleby w latach 2010. w bardzo wyraźny sposób przyczyniła się do zmiany w kompozycji gatunkowej warstwy zielnej lasów bukowych przez eliminację gatunków wymagających gleby o wysokiej wilgotności.

9.1.2. ZMIANY RÓŻNORODNOŚCI ROŚLINNOŚCI ZIELNEJ POMIĘDZY OKRESAMI BADAWCZYMI

Różnorodność alfa tylko nieznacznie wzrosła pomiędzy latami 1970. - 2000., natomiast znacznie spadła pomiędzy latami 2000. - 2010. Zmiany różnorodności beta pomiędzy kolejnymi okresami badawczymi (wzrost w 2010.) były statystycznie istotne. Niespójność między pokazanymi wzorcami różnorodności roślin zielnych wskazują na to, że różnorodność alfa i beta reaguje odwrotnie na zmiany w prowadzonej gospodarce leśnej, przy czym różnorodność beta jest bardziej na te zmiany wrażliwa (**Publikacja 2**). Istnieją dwa możliwe wyjaśnienia spadku miar różnorodności alfa. Pierwsze wywodzi się z hipotezy kompromisu między obszarem a heterogenicznością (*area heterogeneity* *trade-off hypothesis*; Allouche i in. 2012), która sugeruje, że zwiększenie heterogeniczności siedlisk na określonym obszarze może spowodować spadek bogactwa gatunków, ponieważ każdy wzrost heterogeniczności prowadzi do zmniejszenia efektywnej powierzchni dostępnej dla gatunku, zwiększając w ten sposób prawdopodobieństwo losowego wymierania. W latach 2010. stwierdzono znacznie większą heterogeniczność siedlisk niż w przeszłości. Zgodnie z powyższą hipotezą, ten wzrost heterogeniczności siedlisk mógłby zwiększyć lokalne wymieranie gatunków, zwłaszcza tych związanych z typowymi siedliskami lasów bukowych. Po drugie mogło to być spowodowane zmniejszeniem ogólnej liczebności niektórych gatunków w zbiorowiskach, a co za tym idzie rzadszym ich występowaniem pod wpływem intensywniejszego użytkowania lasu (Karp i in. 2012).

Przedstawione wyniki pokazały, że czasowe zmiany w różnorodności wykryte poprzez porównanie zapisów z dwóch okresów badawczych mogą ukryć rzeczywisty przebieg zmian lub przyczynić się do błędnej interpretacji trendu długoterminowych zmian w roślinności zielnej i w konsekwencji prowadzić do błędnej oceny stanu różnorodności lasów.

9.2. ZMIANY W KOMPOZYCJI GATUNKOWEJ I RÓŻNORODNOŚCI ROŚLINNOŚCI ZIELNEJ MIĘDZY STADIAMI ROZWOJOWYMI LASU

9.2.1. ZMIANY KOMPOZYCJI GATUNKOWEJ ROŚLINNOŚCI ZIELNEJ

Drzewostany w stadium dorastania charakteryzują się wysokim zwarciem oraz wysokim tempem pobierania składników pokarmowych. W takiej sytuacji dochodzi do ograniczenia możliwości pobierania tych składników przez roślinność zielną (Cole i Rapp 1981). Ponadto w młodych drzewostanach korzenie silnie konkurują o składniki odżywcze i wodę, ograniczając ich dostęp dla roślin zielnych i zakwaszając glebę (Coomes i Grubb 2000; Augusto i in. 2002, DeYoung 2016). Brak luk w zwartym drzewostanie bukowym i niska wilgotność gleby zmniejsza tempo rozkładu ściółki powodując, że jej ilość jest znacznie większa niż w pozostałych stadiach (Barbier i in., 2008; Durak i in. 2021). Gromadząca się gruba warstwa ściółki bukowej przyczynia się do obniżenia pH i zmniejszenia ilości składników pokarmowych w wierzchniej warstwie gleby (Barbier i in. 2008). Wydaje się więc, że wymienione czynniki ten wpłynęły na stwierdzoną w badanych lasach dużą zmienności wymagań siedliskowych gatunków roślin z warstwy zielnej. Znajdują one również odzwierciedlenie w zestawie gatunków wskaźnikowych wyróżnionych dla stadium dorastania. Gatunki te preferują siedliska zacienione i mniej żyzne (np. *Polygonatum multiflorum*, *Luzula pilosa* i *Festuca drymeia*).

Sytuacja zmienia się w stadium optymalnym. W drzewostanie pojawiają się luki. Zmniejsza się wskaźnik zadrzewienia, konkurencja o wodę i zasoby pokarmowe (DeYoung 2016), wzrasta ilość martwego drewna oraz ilość światła na dnie lasu (Krishna i Mohan 2017; Durak i in. 2021). W efekcie zwiększa się ilość dostępnych dla roślin składników pokarmowych i pH gleby. Stwarza to optymalne warunki rozwoju gatunków typowych dla żyznych buczyn (np. *Dentaria bulbifera*, *Lunaria rediviva*, *Symphytum cordatum*).

W stadium terminalnym wskaźnik zadrzewienia był najniższy, podobnie jak pokrycie warstwy drzew. Natomiast ilość martwego drewna była największa. Zmniejszenie pokrycia warstwy drzew znacznie zwiększyło dopływ światła i wody do dna lasu oraz przyspieszyło rozkład nagromadzonej materii organicznej, co przy wysokim poziomie zakłóceń środowiskowych sprzyjało gatunkom związanym ze śródleśnymi prześwietleniami (zwłaszcza *Rubus hirtus*, *Senecio nemorensis* i *S. fuchsii*) oraz gatunków związanych z prześwietleniem śródleśnymi (porębowych) np. R*umex obtusifolius*), a także rosnącym na obrzeżach lasu np. *Mycelis muralis*.

Roślinność runa leśnego stadiów rozwojowych karpackich lasów bukowych różni się ze względu na realizowane strategie życiowe (C-S-R). Pomiędzy stadium dorastania a stadium optymalnym dominująca strategia R-C zmieniła się na C-R, a następnie na R-C-S w stadium terminalnym. Wydaje się, że dominacja strategii C w stadium optymalnym jest efektem wysokiej stabilności siedliskowej tego etapu rozwoju lasu. Z drugiej strony wzrost udziału tolerancji na stres i spadek konkurencyjności w stadium terminalnym mógł wiązać.

9.2.2. ZMIANY RÓŻNORODNOŚCI ROŚLINNOŚCI LEŚNEJ

W latach 1970. drzewostany były w młodszych klasach wieku, prawie 1/3 powierzchnia badawczych znajdowała się w stadium dorastania. Wówczas roślinność runa charakteryzowały się niską równomiernością rozmieszczenia gatunków oraz dużą liczbą gatunków w zdjęciach fitosocjologicznych. Następnie w latach 2000. gdy dominowało stadium optymalne i presja ze strony gospodarki leśnej, a także ubocznego użytkowania lasu (grabienie ściółki, zbiór chrustu na opał) spadła, zmniejszyło się zróżnicowanie przestrzenne siedlisk i wzrosła ich stabilność (Glatzel 1991; Durak i Holeksa 2015). W porównaniu z latami 1970. różnorodność beta była mniejsza, co sugeruje homogenizację składu gatunkowego roślinności zielnej. W ostatnim okresie badań (2010.) dominowało stadium terminalne. W porównaniu ze wcześniejszymi okresami badań, różnorodność alfa spadła.

Wyniki wskazują na istotną rolę wieku i struktury przestrzennej drzewostanów w regulowaniu składu gatunkowego i różnorodności roślinności runa w lasach bukowych w polskiej części Karpat Wschodnich, w których prowadzi się rębnie stopniowe.

9.3. CZASOWE ZMIANY W KOMPOZYCJI GATUNKOWEJ I RÓŻNORODNOŚCI WARSTWY ZIELNEJ W KONTEKŚCIE STADIÓW ROZWOJOWYCH

W latach 1970. lasy były stosunkowo młode i miały mniejszą zasobność. Intensywność gospodarki leśnej była największa oraz istniało pozaprodukcyjne wykorzystanie lasu - zwłaszcza przez wypas bydła, zbieranie drewna opałowego i grabienie ściółki (Glatzel 1991, Durak i Holeksa 2015). Stąd lasy z lat 1970. dobrze wyróżniała obecność gatunków o niskich wymaganiach świetlnych i troficznych. Wymienione powyżej zakłócenia spowodowały duże zróżnicowanie siedlisk, co nałożyło się na omówiony wcześniej wpływ konkurencji ze strony młodych drzewostanów. W efekcie roślinność zielna charakteryzowała się niską równomiernością rozmieszczenia gatunków oraz dużą liczbą gatunków na powierzchniach badawczych.

W latach 2000. średni wiek drzewostanów na powierzchniach badawczych przekraczał 100 lat, a zadrzewienie i zasobność była największa. W porównaniu do okresu 1970. presja ze strony produkcyjnego i pozaprodukcyjnego wykorzystania lasu znacznie się zmniejszyła, przyczyniając się do zmniejszenia zróżnicowania przestrzennego siedlisk i wzrostu ich stabilności (Durak i Holeksa 2015). Złożyła się na to mniejsze oddziaływanie gospodarki leśnej oraz dominacja stadium optymalnego. W porównaniu do okresu 1970. wzrósł udział gatunków prześwietleń śródleśnych, na co mogło wpłynąć powstawanie luk w drzewostanie. W warstwie zielnej stwierdzono gatunki cienioznośne (np. *Lysimachia nemorum*, *Paris quadrifolia*) oraz preferujące gleby wilgotne (np. *Impatiens noli-tangere*, *Veronica montana* i *Stellaria nemorum*). W porównaniu z latami 1970. różnorodność beta zmniejszyła się, co sugeruje homogenizację składu gatunkowego.

W latach 2010. średni wiek drzewostanów przekroczył 113 lat, wskaźnik zadrzewienia i zasobność zmniejszyła się w porównaniu z poprzednim okresem badawczym. Dominowało stadium terminalne. W rezultacie w porównaniu ze wcześniejszymi okresami spadła: różnorodność alfa, liczba gatunków (w tym gatunków starych lasów i gatunków charakterystycznych dla żyznych buczyn), liczba gatunków preferujących zacienione i wilgotne siedliska, oraz gatunków siedlisk żyznych i o wysokim pH gleby (np. *Paris quadrifolia*, *Pulmonaria obscura*, *Anthriscus nitida*). Zmiany w roślinności były silnie powiązane ze zmianami struktury drzew i krzewów. Na taki mechanizm zwracali uwagę też inni autorzy (np. Ujházy i in. 2005; Šamonil i Vrška 2007).

W każdym okresie badawczym stwierdzono wszystkie trzy stadia rozwojowe drzewostanu. Jednak z upływem czasu dochodziło do przejścia pomiędzy stadiami na poszczególnych powierzchniach badawczych. Zmniejszył się udział stadium dorastania (o znacznym udziale w latach 1970.) i optymalnego (panującego w latach 2000.), a zwiększył udział stadium terminalnego (dominującego w 2010.). Wynika z tego, że roślinność runa poszczególnych okresów badawczych była w dużym stopniu zależna od stadium rozwoju lasu.

Wykazana dominacja jednego stadium rozwojowego lasu w poszczególnych okresach badawczych powodowało, że zróżnicowanie struktury drzewostanów było niewielkie w skali regionalnej. Taka niewielka zmienność stadiów rozwojowych drzewostanu w skali regionalnej została zidentyfikowana jako zagrożenie przyczyniające się do zmniejszenia bioróżnorodności (Schall i in. 2018).

10. PODSUMOWANIE I REKOMENDACJE

Długoterminowe zmiany roślinności runa lasów bukowych w polskiej części Karpat Wschodnich są silnie zależne od stadium rozwoju drzewostanu i prowadzonej gospodarki leśnej. Widoczny jest również wpływ zmian klimatu. Czynniki takie jak zmiana struktury wiekowej drzewostanu, sposób prowadzenia działań gospodarczych, zmiana warunków klimatycznych tj. wzrost średniej temperatury i spadek średniej sumy opadów w okresie wegetacyjnym na przestrzeni ponad 40 lat spowodowały zmiany kompozycji gatunkowej i różnorodności roślin zielnych wschodnio karpackich lasów bukowych.

Stopniowe przejście drzewostanów ze stadium dorastania, a dalej optymalnego (kolejno lata 1970. i 2000.) do stadium terminalnego (2010.) wpłynęło na zmianę warunków siedliskowych. Wyraźnie dało się to zauważyć podczas analizy ekologicznych grup gatunków, strategii życiowych roślin a także gatunków diagnostycznych dla buczyn. Stadium optymalne zapewnia warunki siedliskowe sprzyjające rozwojowi roślin zielnych typowych dla lasów bukowych, wśród których dużą rolę odgrywa strategia C.

W starzejących się buczynach odnotowano spadek różnorodności alfa (mniejsza liczba gatunków) i wzrost różnorodności beta (większe zróżnicowanie pomiędzy powierzchniami badawczymi). Przyczyną było uproszczenie składu gatunkowego drzewostanów oraz wzrost zaburzeń na skutek zaawansowanych procesów odnawiania lasu.

Mając na uwadze prowadzenie zrównoważonej gospodarki leśnej w odniesieniu do roślinności zielnej należałoby uwzględnić następujące postulaty. Po pierwsze, ponieważ mozaika różnych klas wieku drzewostanu ma duże znaczenie dla różnorodności biologicznej regionu (Schall i in. 2018), zarządzający lasami powinni zapewnić tworzenie i utrzymanie drzewostanów o bardziej równomiernym udziale wszystkich stadiów rozwojowych lasu. Po drugie, zróżnicowanie wiekowe drzewostanów powinno być planowane nie tylko w skali lokalnej (np. w obrębie nadleśnictwa) ale również w skali regionalnej.

11. WNIOSKI KOŃCOWE

Na podstawie przedstawionej pracy wyciągnięto następujące wnioski:

1) Kompozycja gatunkowa i różnorodność roślinności runa lasów bukowych w polskiej części Karpat wschodnich podlegały istotnym przemianom na przestrzeni ostatnich ponad 40 lat.

2) Struktura drzewostanu kreowana przez sposób prowadzonej gospodarki leśnej istotnie wpływa na kompozycję gatunkową i różnorodność roślinności runa lasów bukowych.

3) W optymalny stadium rozwoju drzewostanu występują warunki siedliskowe najdogodniejsze dla rozwoju gatunków roślin zielnych typowych dla karpackich lasów bukowych.

4) Długoterminowe zmiany zachodzące w roślinności runa lasów bukowych w polskich Karpatach Wschodnich w dużym stopniu zależą od stadium rozwoju drzewostanu.

5) Ważną rolę w długoterminowych zmianach kompozycji gatunkowej i różnorodności roślinności warstwy runa mogą odgrywać związane z rozwojem drzewostanu procesy o charakterze cyklicznym.

6) Negatywny wpływ zmian klimatu na roślinność warstwy runa będzie się zwiększał w końcowych stadiach rozwoju lasów bukowych wraz z nasileniem procesów odnawiania drzewostanu.

12.PIŚMIENNICTWO

Allouche, O.; Kalyuzhny, M.; Moreno-Rueda, G.; Pizarro, M.; Kadmon, R. 2012. Area-heterogeneity tradeoff and the diversity of ecological communities. Proc. Nat. Acad. Sci. USA. 109, 17495-17500.

Augusto L.; Ranger J.; Binkley D.; Rothe A., 2002. Impact of several common tree species of European temperate forests on soil fertility. Ann. For. Sci. 59, 233-253.

Augusto, L.; Dupouey, J.; Ranger, J. 2003. Effects of tree species on understory vegetation and environmental conditions in temperate forests. Ann. For. Sci. 60, 823-831.

Aussenac, G. 2000. Interaction between forest stands and microclimate: Ecophysiological aspects and consequences for silviculture. Ann. For. Sci. 57 (3), 287-301.

Baeten, L.; Bauwens, B.; De Schrijver, A.; De Keersmaeker, L.; Van Calster, H.; Vandekerkhove, K.; Roelandt, B.; Beeckman, H.; Verheyen, K. 2009. Herb layer changes (1954–2000) related to the conversion of coppice-withstandards forest and soil acidification. Appl. Veg. Sci.

Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134-143.

Barbier, S.; Gosselin, F.; Balandier, P. 2008. Influence of tree species on understory vegetation diversity and mechanisms involved - a critical review for temperate and boreal forests. For. Ecol. Manag. 254, 1-15.

Begehold, H.; Rzanny, M.; Flade, M. 2015. Forest development phases as an integrating tool to describe habitat preferences of breeding birds in lowland beech forests. J. Ornithol. 156, 19-29.

Bengtsson, J.; Nilsson, S.G.; Franc, A.; Menozzi, P. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. For. Ecol. Manag.132, 39-50.

Bergstedt, J.; Hagner, M.; Milberg, P. 2008. Effects on vegetation composition of a modified forest harvesting and propagation method compared with clear-cutting, scarification and planting. Appl. Veg. Sci. 11, 159-168.

Bosela, M.; Štefančík, I.; Petráš, R.; Vacek, S. 2016. The effects of climate Warming on the growth of European beech forest depend critically on thinning strategy and site productivity. Agric. For. Meteorol. 222, 21-31.

Braun-Blanquet, J. 1964. Pflanzensoziologie. Springer-Verlag, Wien-New York, Grundzüge der Vegetationskunde.

Bürgi, M.; Li, L.; Kizos, T. 2015. Exploring links between culture and biodiversity: Studying land use intensity from the plot to the landscape level. Biodivers. Conserv. 24, 3285-3303.

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.

Cole, D. W.; Rapp, M. 1981. Elemental cycling in forest ecosystems. Pages 341–409 in D. E. Reichle, editor. Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, UK.

Coomes, D.A.; Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecol. Monogr. 70, 171-207.

CORINE land Cover-CLC. Available online: https://clc.gios.gov.pl (accessed on 16 March 2021).

Depauw, L.; Perring, M.P.; Landuyt, D.; Maes, S.L.; Blondeel, H.; De Lombaerde, E.; Brūmelis, G.; Brunet, J.; Closset-Kopp, D.; Czerepko, J.; Decocq, G., Ouden, J., Gawryś, R., Härdtle, W., Hédl, R., Heinken, T., Heinrichs, S., Jaroszewicz, B., Kopecký, M., Liepiņa, I., Macek, M., Máliš, F., Schmidt, W., Smart, S.M., Ujházy, K., Wulf, M., Verheyen, K. 2019. Light availability and land-use history drive biodiversity and functional changes in forest herb layer communities. J. Ecol. 108, 1411-1425.

De Lombaerde, E.; Verheyen, K.; Perring, M.P.; Bernhardt-Römermann, M.; Van Calster, H.; Brunet, J.; Chudomelová, M.; Decocq, G.; Diekmann, M.; Durak, T.; Hédl, R., Heinken, T., Hommel, P., Jaroszewicz, B., Kopecký, M., Lenoir, J., Macek, M., Máliš, F., Mitchell, F.J.G, Naaf, T., Newman, M., Petřík, P., Reczyńska, K., Schmidt, W., Świerkosz, K., Vild, O., Wulf, M., Baeten, L. 2018. Responses of competitive understorey species to spatial environmental gradients inaccurately explain temporal changes. Basic Appl. Ecol. 30, 52-64.

DeYoung, J. 2016. Forest Measurements: An Applied Approach - Open Oregon Educational Resources.

Diekmann, M. 2003. Species indicator values as an important tool in applied plant ecology a review. Basic Appl. Ecol. 4, 493-506.

Dittrich, S.; Hauck, M.; Jacob, M.; Rommerskirchen, A.; Leuschner, C. 2012. Response of ground vegetation and epiphyte diversity to natural age dynamics in a Central European mountain spruce forest. J. Veg. Sci. 24, 675-687.

Dufrene, M.; Legendre, P. 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. 67, 345-366.

Durak, T.; Holeksa, J. 2015. Biotic homogenisation and differentiation along a habitat gradient resulting from the ageing of manager beech stands. For. Ecol. Manag. 351, 47-56

Durak, T.; Durak, R. 2015. Vegetation changes in meso-and eutrophic submontane oak–hornbeam forests under long-term high forest management. For. Ecol. Manag. 354, 206-214.

Durak, T.; Durak, R.; Węgrzyn, E.; Leniowski, K. 2015. The impact of changes in species richness and species replacement on patterns of taxonomic homogenization in the Carpathian forest ecosystems. Forests. 6, 4391-4402.

Durak, T.; Bugno-Pogoda, A.; Durak, R. 2021. Application of forest inventories to assess the forest developmental stages on plots dedicated to long-term vegetation studies. For. Ecol. Manag. 489, 119041.

Dzwonko, Z. 1977. Forest communities of the Gory Słonne Range (Polish Eastern Carpathians). Fragm. Flor. Geobot. 23, 161-200.

Dzwonko, Z.; Loster, S. 2001. Wskaźnikowe gatunki roślin starych lasów i ich znaczenie dla ochrony przyrody i kartografii roślinności. IGiPZ PAN. Pr. Geogr. 178, 120-132.

Ellenberg, H.; Weber, H.E.; Düll, R.; Wirth, V.; Werner, W.; Paulissen, D. 1992. Zeigerwerte von Pflanzenin Mitteleuropa. Scripta Geobot. 18, 1-248.

Ellenberg, H.; Leuscher, C. 2010. Vegetation Mitteleuropas mit den Alpen in Ökologischer, Dynamischer und Historischer Sicht; Ulmer: Stuttgart, Germany.

Ewald, J.; Jehl, H.; Braun, L.; Lohberger, E. 2011. Die Vagetation des Nationalparks BayerischerWald als Ausdruck von Standort und Walddynarnik. Tuexenia. 31, 9-38.

Facelli, J.M.; Pickett, S.T.A. 1991. Plant litter: Its dynamics and effects on plant community structure. Bot. Rev. 57, 1-32.

Faliński 2012. Przewodnik do długoterminowych badań ekologicznych. PWN. Warszawa.

Felsmann, K.; Baudis, M.; Kayler, Z.E.; Puhlmann, H.; Ulrich, A.; Gessler, A. 2018. Responses of the structure and function of the understory plant communities to preciptation reduction across forest ecosystems in Germany. Ann. For. Sci. 75, 3.

Franklin, J.; Serra-Diaz, J.; Syphard, A.; Regan, H. 2016. Global change and terrestrial plant community dynamics. PNAS 113 (14), 3725-3734.

Glatzel, G. 1991. The impact of historic land use and modern forestry on nutrient relations of Central European forest ecosystems. Fertil. Res. 27, 1-8.

Gotelli, N.J.; Colwell, R.K. 2001. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecol. Lett. 4, 379-391.

Grgic, T.; Kos, I. 2005. Influence of forest development phase on centipede diversity in managed beech forest in Slovenia. Biodivers. Conserv. 14 (8), 1841-1862.

Grime, J.P. 1977. Evidence for the existence of three primary strategies 600 in plants and its relevance to ecological and evolutionary theory. American Naturalist. 111, 1169-1194.

Grime, J.P. 2001. Plant Strategies, Vegetation Processes and Ecosystem Properties, 2nd edn. Wiley, Chichester.

Hammer, O.; Harper, D.A.T.; Ryan, P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontol. Electron. 4, 1-9.

Heinrichs, S.; Winterhoff, W.; Schmidt, W. 2012. Vegetation dynamics of beech forests on limestone in central Germany over half a century–Effects of climate change, forest management, eutrophication or game browsing? Biodivers. Ecol. 4, 49–61.

Heinrichs, S.; Schmidt, W. 2017. Biotic homogenization of herb layer composition between two contrasting beech forest communities on limestone over 50 years. Appl. Veg. Sci. 20, 271-281.

Hermy, M.; Honnay, O.; Firbank, L.; Grashof-Bokdam, C.; Lawesson, J.E. 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biol. Conserv. 91, 9-22.

Instytut Meteorologii i Gospodarki Wodnej - Państwowy Instytut Badawczy. Available online: https://meteomodel.pl (accessed on 16 March 2021).

Helmy, N.; Essl, F.; Mirtl, M.; Dirnoböck, T. 2017. Multiple environmental changes drive forest floor cegetation in a temperate mountain forest. Ecol. Evol. 7, 2155-2168.

Jacob, M.; Weland, N.; Platner, C.; Schaefer, M.; Leuschner, C.; Thomas, F.M. 2009. Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. Soil Biol. Biochem. 41, 2122.

Jaworski, A.; Kołodziej, Z. 2004. Beech (Fagus sulvatica L.) forest of a selection structure in the Bieszczady Mountains (Southeastern Poland). J. For. Sci. 50, 301-312.

Jaworski, A. 2018. Hodowla Lasu. Tom, I. Sposoby Zagospodarowania, Odnawianie Lasu, Przebudowa i Przemiana Drzewostan*ó*w; Powszechne Wydawnictwo Rolnicze i Leśne. Warszawa.

Karp, D.S.; Rominger, A.J.; Zook, J.; Ranganathan, J.; Ehrlich, P.R.; Daily, G.C. 20012. Intensive agriculture erodes b-diversity at large scales. Ecol. Lett. 15, 963-970.

Kozak, J. 2010. Forest Cover Changes and Their Drivers in the Polish Carpathian Mountains since 1800. In Reforesting Landscapes Linking Pattern and Process; Nagendra, H., Southworth, J., Eds.; Springer: Dordrecht, The Netherlands; Heidelberg, Germany; London, UK; New York, NY, USA.

Kozak, J.; Szwagrzyk, M. 2016. Have there been forest transitions? Forest transition theory revisited in the context of the Modifiable Areal Unit Problem. R. Geogr. Soc. 48, 504-512.

Kozak, J.; Ziółkowska, E.; Vogt, P.; Dobosz, M.; Kaim, D.; Kolecka, N.; Ostafin, K. 2018. Forest-Cover Increase Does Not Trigger Forest-Fragmenntation Decrease: Case Study from the Polish Carpathians. Sustainability 10, 1472.

Koop, H., 1989. Forest dynamics, SILVI-STAR: a comprehensive monitoring system. Springer Verlag, Berlin.

Korpel, S. 1995. Die Urwalder der Westkarpaten. Gustav Fischer Verlag, Stuttgart.

Krishna M.P.; Mohan M. 2017. Litter decomposition in forest ecosystems: a review. Energy Ecol. Environ. 2, 236-249.

Krupková, L.; Havránková, K.; Krejza, J.; Sedlák, P.; Marek, M.V. 2019. Impact of water scarcity on spruce and beech forests. J. For. Res. 30, 899-909.

Larrieu, L.; Cabanettes, A.; Gonin, P.; Lachat, T.; Paillet, Y.; Winter, S.; Bouget, C.; Deconchat, M. 2014. Deadwood and tree microhabitat dynamics in unharvested temperate mountain mixed forests: a life-cycle approach to biodiversity monitoring. For. Ecol. Manag. 334, 163-173.

Langenbruch, C.; Helfrich, M.; Flessa, H. 2012. Effects of beech (Fagus sylvatica), ash (Fraxinus excelsior) and lime (Tilia spec.) on soil chemical properties in a mixed deciduous forest. Plant Soil. 352, 389-403.

Leibundgut, H., 1993. Europaische Urwalder—Wegweiser zur naturnahen Waldwirtschaft. Paul Haupt, Bern.

Majchrowska, A. 2018. The History of State Forest and Forestry in Poland. Manag. North. Eur. For. 12, 318-358.

Matlack, G.R.; Monde, J. 2004. Consequences of low mobility in spatially and temporally heterogeneous ecosystems. J. Ecol. 92, 1025-1035.

Matlack, G.R. 2005. Slow plants in a fast forest: Local dispersal as a predictor of species frequencies in a dynamic landscape. J. Ecol. 93, 50-59.

Matuszkiewicz, W. 2001. Przewodnik do Oznaczania Zbiorowisk Roślinnych Polski. [A Guide for the Identification of Polish Plant Communities]; Wydawnictwo Naukowe PWN: Warszawa.

Melo, M.; Lapin, M.; Kapolková, H.; Pecho, J.; Kružicová, A. 2013. Climate Trends in the Slovak Part of the Carpathians. In The Carpathians: Integrating Nature and Society Towards Sustainability. Environmental Science and Engineering; Kozak, J., Ostapowicz, K., Bytnerowicz, A.,Wyz˙ga, B., Eds.; Springer: Berlin/Heidelberg, Germany.

Meyer, P., 1999. Bestimmung der Waldentwicklungsphasen und der Texturdiversitat in Naturwaldern. Allg. F. u. J. Ztg. 170, 203-211.

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. For. Ecol. Manag. 319, 51-61.

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, T.,M., Schmidt, W., Standovár, T., Tóthmérész, 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.

Parpan, V.I.; Stojko, S.M.; Parpan, T.V. 2013. Phytocoenotical and ecological characterization of beech forests (Fagus sylvaticae L.) of Ukraine and possibility to expand their area due to global Warming. Infrastruktura i Ekologia Terenów Wiejskich. 2, 29-44.

Pawłowski B. 1977. Skład i budowa zbiorowisk roślinnych oraz metody ich badania. W: Szafer W., Zarzycki K. [red.]. Szata roślinna Polski. t. I. PWN, Warszawa. 237-279.

Perring, M.P.; Bernhardt-Römermann, M.; Baeten, L.; Midolo, G.; Blondeel, H.; Depauw, L.; Landuyt, D.; Maes, S.L.; De Lombaerde, E.; Caròn, M.M.; Vellend, M.; Brunet, J.; Chudomelová, M.; Decocq, G.; Diekmann, M.; Dirnböck, T.; Dörfler, I.; Durak, T.; Pierce, S.; Brusa, G.; Vagge, I.; Cerabolini, B.E.L. 2013. Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. Funct. Ecol. 27, 1002-1010.

Pierce, S.; Negreiros, D.; Cerabolini, B.E.L.; Kattge, J.; Díaz, S.; Kleyer, M.; Shipley, B.; Wright, S.J.; Soudzilovskaia, N.A.; Onipchenko, V.G.; Van Bodegom, P.M.; Frenette-Dussault, C.; Weiher, E.; Pinho, B.X.; Cornelissen, J.H.C.; Grime, J.P.; Thompson, K.; Hunt, R.; Wilson, P.J.; Buffa, G.; Nyakunga, O.C.; Reich, P.B.; Caccianiga, M.; Mangili, F.; Ceriani, R.M.; Luzzaro, A.; Brusa, G.; Siefert, A.; Barbosa, N.P.U.; Chapin, F.S.; Cornwell, W.K.; Fang, J.; Fernandes, G.W.; Garnier, E.; Le Stradic, S.; Peñuelas, J.; Melo, F.P.L.; Slaviero, A.; Tabarelli, M.; Tampucci, D. 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. Funct. Ecol. 31, 444-457.

Rackham, O. 2008. Ancient woodlands: Modern threats. New Phytol. 180, 571-586.

Ritter, E.; Dalsgaard, L.; Einhorn, K., 2005. Light, temperature and soil moisture regimes following gap formation in a semi-natural beech-dominated forest in Denmark. For. Ecol. Manag. 206, 15-33.

Rooney, T.P.; Wiegmann, S.M.; Rogers, D.A.;Waller, D.M. 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conserv. Biol. 18, 787-798.

Rozkrut, D. 2020. Roczniki Statystyczne Leśnictwa. GUS. Warszawa.

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.

Skiba, S.; Drewnik, M. 2003. Soil map of the polish carpathian mountains. Rocz. Bieszcz. 11, 15-20.

Standovar, T.; Kenderes, K. 2003. A review on natural stand dynamics in Beechwods of East Central Europe. Appl. Ecol. Environ. Res. 1, 19-46.

Šamonil, P.; Vrška, T. 2007. Trends and cyclical changes in natura l fir-beech Forests at the north western edge of the Ca rpathians. Folia Geobotanica. 42, 337-361.

Tabaku, V. 2000. Struktur von Buchen-Urwaldern in Albanien im Vergleich mit deutschen Buchen-Naturwaldreservaten und- Wirtschaftswaldern. PhD thesis. Cuvillier Verlag, Gottingen.

Thom, D.; Sommerfeld, A.; Sebald, J.; Hagge, J.; Müller, J.; Seidl, R. 2020. Effect of disturbance patterns and deadwood on the microclimate in European beech forests. Agric. For. Meteorol. 291, 108066.

Ujházy, K.; Križová, E.; Vančo, M.; Freňaková, E.; Ondruš, M. 2005. Herb layer dynamics of primeval fir-beech forests in central Slovakia. In: Commarmot, B.; Hamor, F. D. (eds):

Ujházy, K.; Hederová, L.; Máliš, F.; Ujházyová, M.; Bosela, M.; Čiliak, M. 2017. Overstorey dynamics controls plant diversity in age-class temperate forests. For. Ecol. Manag. 391, 96-105.

Van Calster, H.; Baeten, L.; De Schrijver, A.; De Keersmaeker, L.; Rogister, J.E.; Verheyen, K., Hermy, M. 2007. Management driven changes (1967–2005) in soil acidity and the understorey plant community following conversion of a coppice-with-standards forest. For. Ecol. Manag. 241, 258–271.

Vacek, S.; Cĕrný, T.; Vacek, Z.; Podrázský, V.; Mikeska, M.; Králícĕk, I. 2017. Long-term changes in vegetation annd site conditions in beech and spruce forest of lower mountains ranges of Central Europe. For. Ecol. Manag. 398, 75-90.

Vacek, S.; Prokůpková, A.; Vacek, Z.; Bulušek, D.; Šimůnek, V.; Králíček, I.; Prausová, R.; Hájek, V. 2019. Growth response of mixed beech forests to climate change, various management and game pressure in Central Europe. J. For. Sci. 65, 331-345.

Watt, A.S., 1947. Pattern and process in the plant community. J. Ecol. 35, 1-22.

Winter, S.; Brambach, F. 2011. Determination of a common forest life cycle assessment method for biodiversity evaluation. For. Ecol. Manag. 262 (12), 2120-2132.

Zellweger, F.; De Frenne, P.; Lenoir, J.; Van Gansbeke, P.; Verheyen, K.; Bernhardt-Römermann, M.; Baeten, L.; Hédl, R.; Berki, I.; Brunet, J.; Van Calster, H., Chudomelová, M., Decocq, G., Dirnböck, T., Durak, T., Heinken, T., Jaroszewicz, B., Kopecký, M., Máliš, F., Macek, M., Malicki, M., Naaf, T., Nagel, T.A., Ortmann-Ajkai, A., Petřík, P., Pielech, R., Reczyńska, K., Schmidt, W., Standovár, T., Świerkosz, K., Teleki, B., Vild, O., Wulf, M., Coomes, D. 2020. Forest microclimate dynamics drive plant responses to Warming. Science. 368, 772-775.

OŚWIADCZENIA WSPÓŁAUTORÓW

Rzeszów, dnia 27.05.22

Imię i nazwisko: Anna Bugno-Pogoda

Jednostka: Instytut Biologii i Biotechnologii

Promotor: dr hab. Tomasz Durak, prof. UR

Promotor pomocniczy: brak

OŚWIADCZENIE

W związku z przygotowywaniem przeze mnie rozprawy doktorskiej w formie spójnego tematycznie zbioru artykułów, oświadczam niniejszym, że wkład mojej pracy naukowej, a tym samym pracy pozostałych współautorów w opublikowaniu poniższych artykułów, które zamierzam przedstawić jako własną dysertację doktorską jest następujący:

1. **Bugno-Pogoda, A.**, Durak, R., Durak, T. 2021. Impact of Forest Management on the Temporal Dynamics of Herbaceous Plant Diversity in the Carpathian Beech Forests over 40 Years. *Biology*, 10 (5), 406; https://doi.org/10.3390/biology10050406 (IF2021 = 5,079; Punkty MNiSW2021 = 100)

    - koncepcja badań: 30% - określenie problemu badawczego, jego znaczenia, wyznaczenie celów i hipotez
    - metodyka: 50% udział w opracowaniu metodyki badań
    - praca terenowa: udział w zbiorze danych w latach 2017-2018 – 100%
    - praca laboratoryjna: 100% analizy zebranych w terenie próbek
    - analiza i zestawienie wyników: 50%
    - interpretacja wyników i dyskusja:50%
    - prace nad manuskryptem (draft, wersja końcowa): 40%
    - analiza bibliograficzna:80%
    - proces publikacji (autor korespondencyjny): 0%

    Zatem mój wkład pracy naukowej w przygotowanie manuskryptu wynosi **50%**

    Jako współautor akceptuję przedstawiony przez Panią Annę Bugno-Pogoda udział w przygotowaniu powyżej publikacji naukowej, która stanowić będzie część Jej dysertacji doktorskiej:

    1. Durak Roma (udział 10%)..
    2. Durak Tomasz (udział 40%)..

2. **Bugno-Pogoda, A.**, Durak, T. 2021. Climate and Management Factors Underlying Changes in Beech Forest Herbaceous Layer Plant Communities in the Polish Eastern Carpathians. *Forests*, 12 (11), 1446; https://doi.org/10.3390/f12111446 (IF$_{2021}$ = 2,633; Punkty MNiSW$_{2021}$ = 100)

- koncepcja badań: 60% - określenie problemu badawczego, jego znaczenia, wyznaczenie celów i hipotez
- metodyka: 50% udział w opracowaniu metodyki badań
- praca terenowa: udział w zbiorze danych w latach 2017-2018 – 100%
- praca laboratoryjna: nie dotyczy
- analiza i zestawienie wyników: 70%
- interpretacja wyników i dyskusja:60%
- prace nad manuskryptem (draft, wersja końcowa): 60%
- analiza bibliograficzna:90%
- proces publikacji (autor korespondencyjny): 50%

Zatem mój wkład pracy naukowej w przygotowanie manuskryptu wynosi **60%**

Jako współautor akceptuję przedstawiony przez Panią Annę Bugno-Pogoda udział w przygotowaniu powyżej publikacji naukowej, która stanowić będzie część Jej dysertacji doktorskiej:

1. Durak Tomasz (udział 40%)……………………………………………………………………

3. Durak, T., **Bugno-Pogoda, A.**, Durak, R. 2022. Impact of forest stand development on long-term changes in the herb layer of semi-natural Carpathian beech forests. *Forest Ecology and Managament*, 518, 120233; https://doi.org/10.1016/j.foreco.2022.120233 (IF$_{2021}$ = 3,558; Punkty MNiSW$_{2021}$ = 200)

    - koncepcja badań: 30% - określenie problemu badawczego, jego znaczenia, wyznaczenie celów i hipotez
    - metodyka: 50%- udział w adaptacji metod do oznaczeń
    - praca terenowa: udział w zbiorze danych w latach 2017-2018 – 100%
    - praca laboratoryjna: 100% analizy zebranych w terenie próbek
    - analiza i zestawienie wyników: 50%
    - interpretacja wyników i dyskusja: 40%
    - prace nad manuskryptem (draft, wersja końcowa):40%
    - analiza bibliograficzna:100%
    - proces publikacji (autor korespondencyjny): 0%

Zatem mój wkład pracy naukowej w przygotowanie manuskryptu wynosi **50%**

Jako współautor akceptuję przedstawiony przez Panią Annę Bugno-Pogoda udział w przygotowaniu powyżej publikacji naukowej, która stanowić będzie część Jej dysertacji doktorskiej:

1. Durak Tomasz (40%)……………………………………………………………………………………………
2. Durak Roma (10%)……………………………………………………………………………………………

PUBLIKACJE WCHODZĄCE W SKŁAD ROZPRAWY DOKTORSKIEJ WRAZ Z SUPLEMENTAMI

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Impact of Forest Management on the Temporal Dynamics of Herbaceous Plant Diversity in the Carpathian Beech Forests over 40 Years

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Simple Summary: Vegetation composition and plant diversity of mixed deciduous forests in Europe is strongly linked with the dynamics of the forest stand and/or the regimes of forest management. In this work, we showed the influence of temporal interactions among the changes in the management system—the dominant development stage—the intensity of forest treatments, and herbaceous plant diversity. We argued that different arrangements of these interactions will result in different patterns of change in herbaceous plant diversity. We emphasized the need for careful interpretation of the levels of diversity (α, β) to evaluate the conservation status of forests.

Abstract: In recent years, there has been a growing awareness of the complex dependence of herbaceous plant diversity on forest structure and management. However, among the studies presented so far, those in which the chronosequence (approach based on the assumption of space-for-time substitution) was used, dominate. On the other hand, it is rare to find results based on long-term research on permanent or semi-permanent sampling plots. The aim of this study was to recognize the changes in the vegetation composition and dynamics of various indices of herbaceous plant diversity over 40 years of forest development, and their dependence on forest structure and management. Here we analyzed the temporal dynamics of herbaceous plant diversity in Carpathian fertile beech forests, based on datasets recorded on semi-permanent plots in three censuses (the 1970s, 2000s and 2010s). We checked the temporal changes in alpha, beta, and gamma diversity. Analyses of the plant diversity were performed on the background of changes in forest structure and management systems. We found that the within-plot (alfa diversity) and between-plot (beta diversity) herbaceous plant diversity metrics showed inconsistent patterns along with changes in the forest structure, management systems, and intensity of forest management, during the last 40 years. Temporal changes in the gamma diversity followed the changes in alpha diversity. Although the beta diversity after 40 years is greater than in the past, we argue that the conservation status of habitats typical for well-preserved fertile mountain beech forests has deteriorated due to a decline in the sharing of the diagnostic species of these forests. We showed the importance of the different temporal interactions between the forest structure and management for herbaceous plant diversity. We argue that, in view of the complexity of these processes, it would be a mistake to reject or prioritize alpha or beta diversity measurements to determine the real course of long-term changes in herbaceous plant diversity and to properly assess the state of the forest biodiversity, their conservation status, or conservation action plans. In addition, we need far more data from long-term observations to fully understand the possible relationship patterns between the factors controlling the forest structure and plant diversity.

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1. Introduction

In temperate forests, the herbaceous layer constitutes most of the forest plant diversity and has significant influence on key ecosystem processes, such as nutrient cycling, tree regeneration, and competitive interactions [1]. However, since the second half of the twentieth century, the species composition of European forest herbaceous plant communities has experienced rapid changes, which, very often, have been identified as a threat to the functioning of plant communities and ecosystems and have led to the loss of biodiversity [2–4]. Changes in species composition were caused by the processes changing the environmental conditions, which resulted in the disappearance or spread of species. These changes in the environmental conditions were most often driven by global changes (especially climate changes and air pollutions) or forest management and noncommercial forest human use, such as collecting firewood and raking litter [5,6]. They often led to the spread of habitat generalists or invasive species and the disappearance of habitat specialists. The latter were associated especially with the loss of nitrogen-poor habitats and an increase in temperature. As a result, changes in forest herbaceous plant communities were frequently recognized as directional processes, resulting in a simplification of their species structure and a loss of diversity on different levels of spatial organization [7,8].

Recently, forest ecologists have revealed an increasingly complex picture of the impact of forest structure and forest management on the species composition and diversity of communities [9–12]. It has been shown that the composition of forest communities or diversity were not only dependent on the stands' differentiation in terms of their structure specific for different developmental stages/phases but, also, from the forester-shaped spatial distribution of the stands' developmental stages, as well as the size of the patches occupied by the forest developmental stages/phases. For example, Schall et al. [13] indicated that, on a regional scale, coarse-grained management (shelterwood system) by creating a mosaic of stands in different age classes, can harbor more biodiversity than fine-grained selection systems (resulting in higher within-stand heterogeneity, but low between-stand). Hilmers et al. [10] highlighted the high dependency between the forest developmental stages and biodiversity and underlined that the cyclical impact of forest dynamics (internal drivers) can be misinterpreted as directional impact of the external drivers (e.g., climate change).

In recent decades, in addition to forest management as such, the vertical and horizontal structures of forests are significantly influenced by shifts between the forest management system, implemented to replace intensive forest management strategies with close-to-natural methods [14–17]. Thus, shifts between the forest management system were used to convert low forests (known as coppice forests) into high forests (stands consisting of large, tall, mature trees with a closed canopy). In the case of such conversion of a forest stand, large changes in herbaceous plant diversity could be expected. Indeed, many authors have reported a decrease in the structural and functional plant diversities, as well as in the conservation values of forests [18–20]. However, in the case of changes in the management system in high forests (e.g., changes from clear-cutting to shelterwood or selective-cutting systems), the changes in the forest herbaceous layer are less-recognized. Additionally, less obvious changes can be expected in the forest herbaceous layer than in the case of a converted low forest. For example, Durak and Holeksa [21] found biotic homogenization in forest herbaceous communities in resource-rich habitats and biotic differentiation in resource-poor habitats in aging Carpathian beech forests, where regular shelterwood has been changed to an irregular shelterwood system. These observations are important in the context of the development of age structure of forests throughout Europe. Although the majority of these forests are currently of intermediate age, the proportion/area of late forest developmental stages (e.g., terminal stage) is clearly growing [22]. It follows that the unravelling of the influence of the stand structure on changes in the composition and diversity of the forest herbaceous layer should be considered within the context, of course, of changes in the forest management and stand structure. It should be expected that not only the change in the management method be important; we argue that the impact of change in the management system will depend on the time point in the forest development when the management system was changed, as well as from the developmental stage itself.

Long-term research seems to be the most reliable way of unravelling vegetation responses to temporal changes [23,24]. However, so far, the knowledge gained in the relationship between changes in the forest structure and management (on the one hand) and herbaceous vegetation composition and plant diversity (on the other hand) was mostly based on vegetation records from two time points (e.g., [19,25–27]). Here, we analysed the dynamics of the Carpathian fertile beech forest herbaceous plant diversity (managed semi-natural forests) based on datasets recorded on semipermanent plots in three subsequent censuses (the 1970s, 2000s, and 2010s).

So far, due to the simplicity of the measurements, the effects of forest management on species diversity were studied mostly with the focus on alfa diversity expressed by species richness [28–30]. However, there are three diversity components that depend on the spatial scale: the aforementioned local alpha diversity (measured within locations, in this work—within stands), as well as beta diversity (measured between locations, in this work—between stands) and regional gamma diversity. Beta diversity is known as a fundamental component of biodiversity—decisive for the process of biotic homogenization (decrease of beta diversity, resulting in an increase in species similarity across space over time) [31,32]. The term gamma diversity is defined as the regional species pool. It is assumed that these three diversity components are related to each other and that beta diversity provides a link between the local alpha diversity and regional gamma diversity [33–35]. It transpires, however, that the dependencies between diversity components are not always obvious. For example, Schall et al. [13] showed that the local alfa diversity may hide patterns of remaining diversity components (beta and gamma diversity). Moreover, alfa diversity adopted as an indicator for the conservation status of the forests can lead to the wrong conclusion [11]. Hence, in order to better understand the patterns of herbaceous vegetation in beech forests, we examined all three diversity components. Moreover, to get a sound and relevant measure of alfa diversity as a measure of the conservation status of the forests, in addition to classical alfa indices (Shannon and evenness diversity indices), we expressed alfa diversity as a species richness of ecological groups of species defined as species specialists with high and low habitat requirements. Additionally, to recognize the conservation status of investigated forests, we took into account conservation-relevant species (diagnostic species for beech forests), as well as plant species whose frequencies of occurrence or abundance increased significantly (hereafter, winner species) or decreased (hereafter, loser species) throughout the research period.

Analyses of the herbaceous plant diversity were performed on the background of changes in the stand structure (resulting from the forest stands' development) and management system (from the 1990s, regular shelterwood was replaced by close-to-nature irregular shelterwood silvicultural systems). Therefore, we expected to find a more complex answer to the course of changes that have occurred in herbaceous plant diversity during the past 40 years and their drivers.

We expect that the increased or decreased differentiation of the spatial structure of the forest (forest habitat heterogeneity) will result in a decrease or increase in the resource availability (trade-off between the area available for individual species and habitat heterogeneity on the spatial scale) according to the "area heterogeneity trade-off hypothesis" [36]. Consequently, this may result in a reduction or increment in the size of local populations and an increase or decrease in the likelihood of their stochastic extinction, which will be reflected in the different diversity patterns between vegetation censuses.

The aim of this study was to recognize: (1) temporal dynamics of the herbaceous plant diversity (alpha, beta, and gamma diversity) over 40 years of forest development and management; we expected inconsistencies in the patterns of diversity within and between the vegetation censuses; (2) the relationships between forest structure and management and herbaceous plant diversity on different spatial scales; (3) the contribution of ecological groups of the species to the reaction of herbaceous vegetation to changes in the forest structure and forest management; and the (4) impact of the changes in forest structure and management on the species composition, taking into account winner and loser species, as well as species having important conservation statuses in fertile mountain beech forests (FMBF).

2. Materials and Methods

2.1. Study Area

The study area is located in the Sanocko-Turczańskie Mountains in the Polish Eastern Carpathians (49°33 6.900″ N; 22°20 42.225″ E; Figure 1). This part of the Polish Carpathian Mountains is dominated by brown soils formed from Carpathian flysch [37,38]. The average annual temperature is 7.7 °C, and the annual rainfall is 820.8 mm (data from the station Lesko, 420 m a.s.l., for the period 1966–2018 [39]). The forests are dominated by FMBF (according to the phytosociological classification—*Dentario glandulosae Fagetum* Klika 1927 em. Mat. 1964). The dominant species in these forests is European beech (*Fagus sylvatica*). Moreover, silver fir (*Abies alba*) and sycamore maple (*Acer pseudoplatanus*) may appear in small admixtures. This area is part of the Natura 2000 network ("Ostoja Góry Słonne" PLH180013 and "Góry Słonne" PLB180003).

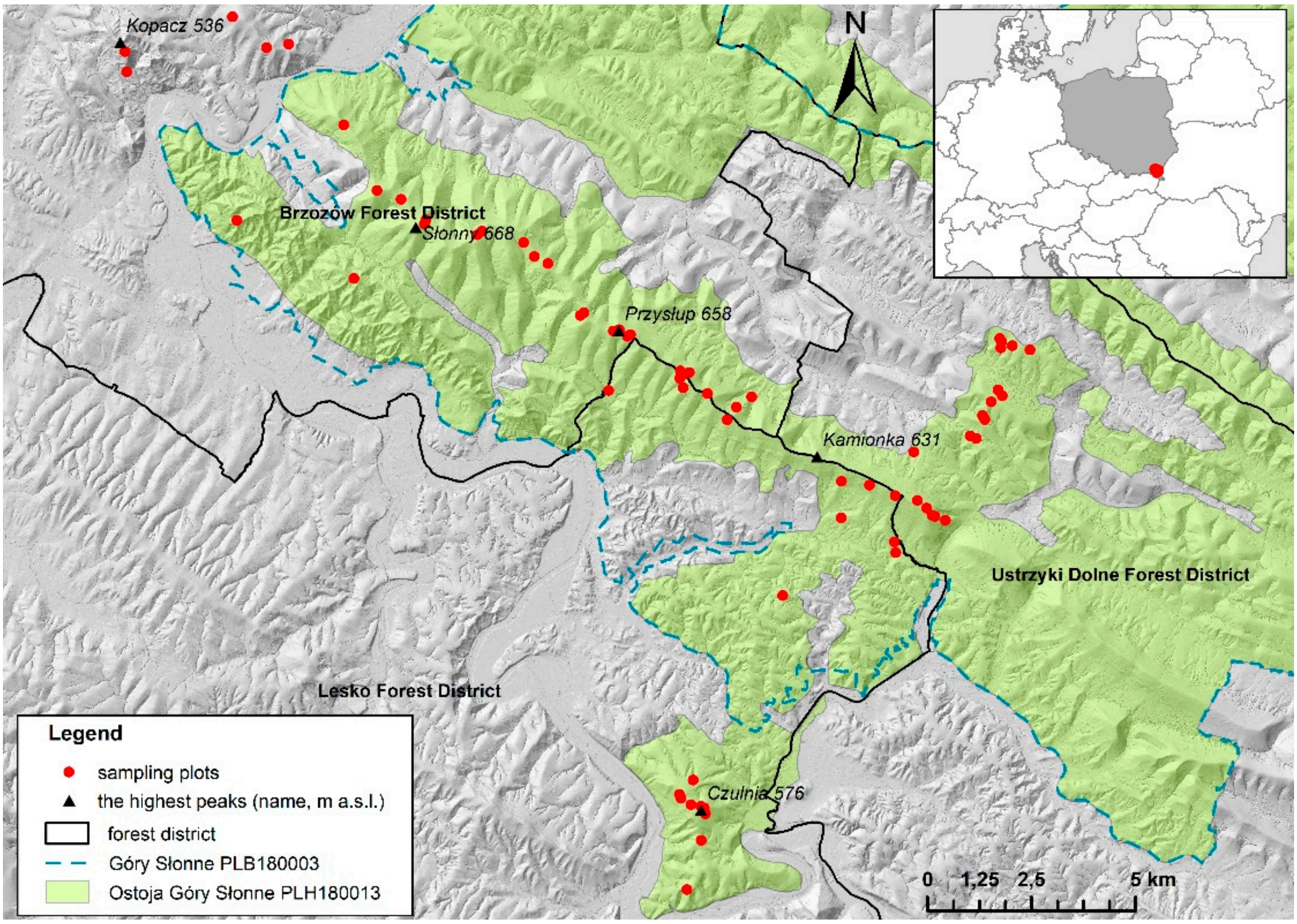

Figure 1. Location of the study site and distribution of semipermanent sampling plots within the study area.

Forests in this region are managed by the Brzozów, Lesko, and Ustrzyki Dolne Forest District. Between the 1950s and 1990s, the forests were regenerated using the regular shelterwood system, the most popular cutting method in the mountainous area of the Polish Carpathians [40]. The regular shelterwood system created even-aged stands with low variation in the tree sizes. At the end of the 1990s, the management system was changed to an irregular shelterwood system, which more efficiently imitates the natural processes occurring in forest ecosystems, creating a closer to nature forest structure (it produces irregular stand structures, even on small spatial scales). This management system, compared to the regular shelterwood system is characterized by an extended rotation age (110–130 years) and a longer regeneration period (from 30 to 50 years). For a more detailed comparison of the two forest management systems, please refer to Table 1.

Table 1. Characteristics of the forest management methods used in the Sanocko-Turczańskie Mountains beech forests.

	Regular Shelterwood System	Irregular Shelterwood Systems
Rotation age	80–110 years	110–130 years
Regeneration period	10–20 years	30–50 years
Regeneration processes	System in which, in order to provide a source of seed and/or protection for regeneration, the mature stand is removed in two or more overstory removal cuttings. The first of which is an establishment cutting to establish the regeneration from the seeds. After 2–5 years, to provide the best conditions for the growth of a new generation of trees partial mature trees, removals are started. After 10–20 years, all the mature trees are removed by a final cut.	In dense stands, foresters choose irregularly distributed plots where, every 3–6 years, they cut a small group of trees, forming small gaps. This cycle is repeated within the previously formed gaps, where another small group of trees are cut, thus expanding the gaps in the stands. Process of expanding the gaps continues throughout the regeneration cycle.
Stand structure	even-aged	uneven-aged

2.2. Data Collection

In our study, three sets of vegetation records were compared. Vegetation records were made according to the Braun-Blanquet method [41] as so-called phytosociological relevés, during three vegetation censuses (1972–1973, 2005–2007, and 2017–2018) on an irregular network of 67 sampling plots (Figure 1). During the second vegetation census, these plots were reestablished, marked by geographic coordinates, and resurveyed [21]. Geographic coordinates of the sampling plots made it possible to locate them extremely accurately during the third vegetation census. After the re-localization of sampling plots, their location was additionally verified using descriptions from the 1970s. We found compliance in the case of all plots. To make the three datasets comparable, during both resurveys, the vegetation records were taken from 67 sampling plots with the same area (usually 200 or 400 m^2) during the growing season, as in the 1970s. Vegetation records contain data on: forest layer coverage, species composition of forest layers, and abundance of plant species in individual forest layers (estimated using the cover–abundance scale). In addition, they contained data on the prevalent height and DBH of trees in the sampling plot. Forest layer coverage and height of trees were measured according to the Braun-Blanquet [41] methodology. Under this approach, the coverage of the tree and shrub layers was estimated on the basis of their vertical projections as a percentage of the sampling plot. Tree height was defined as the most common tree height in the tree layer and was determined based on one measurement per sampling plot. The DBH of a tree (measured at a height of 1.3-m aboveground level) was defined as the most common DBH of a tree in the sampling plot and determined similarly to the height of the tree. Moreover, datasets from the vegetation records were expanded to include the age of stands and the forest management intensity included in the Forest Management Plans as of 1976–1977, 2007–2009, and 2017–2019 (by forest sub-compartments on which individual sampling plots were located). The management plans used were prepared for Forest Districts Brzozów, Lesko, and Ustrzyki Dolne (available in the Regional Directorate of the State Forests in Krosno).

2.3. Data Analysis

In order to ascertain the relationship between forest structure and management and the diversity dynamics of the herbaceous layer, we considered forest structure characteristics, stand age, and intensity of forest management, as well as changes in the forest management system. Forest structure characteristics were measured on the sampling plot level. Tree and shrub (including tree and shrub saplings) layer cover (%), tree height and DBH, and number of species in tree and shrub layers were recorded. Due to a lack of DBH data in records from the 1970s, they were supplemented by data from the oldest available forest inventories (Forest Management Plans from the 1970s). Prior to that, we checked whether the forest inventory data corresponded to the data measured on the sampling plots. For this purpose, we used data from the 2000s. We calculated the average DBH for the data from the sampling plots and corresponding inventory data (average DBH, 49.0 cm and 48.4 cm, respectively). Additionally, we correlated them ($r_s = 0.32$, $p \leq 0.01$). Based on the results, we found that the inventory data sufficiently corresponded to the data from the sampling plots. Moreover, based on Forest Management Plans from the 1970s, 2000s, and 2010s, the age of the stands (mean age for the dominant tree species), as well as the forest management intensity levels, were considered. To reveal changes in the intensity of forest management, the management intensity levels were arranged from the lowest to the highest and ranked on a five-point scale. To emphasize the importance of low, as well as a very high intensity of forest management, the points on this scale were not equidistant: no interference—1, thinning—4, irregular shelterwood treatments lasting 10 years—6, irregular shelterwood treatments lasting 20 years—7, and regular shelterwood treatments—9. All data from the Forest Management Plans were compiled for forest sub-compartments (the basic territorial unit of the State Forests, defined for the needs of forest management) in which the sampling plots were located.

We considered changes in the alpha, beta, and gamma herbaceous plant diversities. For this purpose, we computed the Shannon and evenness diversity indices (α_{Sha} and evenness), Sorensen dissimilarity index (β_{Sor}, total beta diversity) partitioned according to Baselga [42] on the Simpson dissimilarity index (β_{Sim}, species turnover component), and nestedness (β_{nes}, species extinction or colonization component). Gamma diversity (γ) was defined as the total species pool noted in a given census.

To detect the biotic homogenization or differentiation of the herbaceous vegetation, a method based on the average inter-plot dissimilarities was adopted [25,43,44]. Changes were computed as the difference in the pairwise species dissimilarities between the distinct sampling times [45]. To accomplish this, dissimilarity indices (β_{Sor}, β_{Sim}, and β_{nes}) were calculated, for all possible pairs of plots from the 1970s, 2000s, and 2010s. Then, the average dissimilarity indices were calculated for each plot in each of the three vegetation censuses. Differences between the vegetation censuses were evaluated using a several sample repeated-measure ANOVA test with posteriori Tukey's test. We assumed that a decrease or increase in the mean values of the β_{Sor} index would indicate the homogenization or differentiation of vegetation over time. Concurrently, both components of β_{Sor} that quantify the species turnover (species replacement) and nestedness (species richness) can change opposite to each other.

This method, based on the average inter-plot dissimilarities, was also adopted to detect changes in the forest habitat heterogeneity between plots. To reveal the habitat conditions prevailing on sampling plots, we used Ellenberg indicator values (EIVs) for light (L), temperature (T), soil moisture (F), soil reaction (R), and soil nitrogen (N) [46]. Average indicator values were calculated using plant species qualitative (presence/absence) data for sampling plots from each vegetation census. In order to quantify the changes in habitat heterogeneity between the 1970s, the 2000s and 2010s, the abundance-based Morisita-Horn (M-H) dissimilarity index was used [47]. In the case of finding changes in the habitat heterogeneity in one of the study periods, we checked their relationship with changes in the herbaceous plant diversity within-plot ($\Delta\alpha_{Sha}$) and between-plots ($\Delta\beta_{Sor}$). For this purpose, the correlation between $\Delta\alpha_{Sha}$ and $\Delta\beta_{Sor}$ indices and the changes in the M-H coefficients (expressing habitat heterogeneity) in the relevant study period were tested.

At the community level, the herbaceous species frequency of occurrence was compared between the vegetation censuses. Herbaceous species richness, richness of ecological groups of species defined based on high or low requirements for habitat conditions (estimated on the basis of Ellenberg indicator values), and total abundance (sum of abundances of species estimated by the Braun-Blanquet cover-abundance scale transformed to mid-point percentage values) were considered at plot level for each vegetation census. Among the distinguished ecological groups of species were groups of species with high (EIVs ≥ 7, L_H, F_H, R_H, and N_H) and low indicator values (EIVs ≤ 3, L_L, R_L, and N_L). Due to the small number of the species meeting the criteria, we did not consider the F_L group, and the T_H and T_L were expanded to include species with indicator values ≥ 6 and ≤ 4, respectively. At the species level, by comparing the frequency of the occurrence and species abundance between vegetation censuses, we identified the winner and loser plant species groups. To these groups, we included only plant species for which (1) the sum of changes in the frequency of occurrence in the first and second study periods increased or decreased by at least 10%, or (2) the abundance between the three vegetation censuses revealed a significant increase or decrease. Moreover, to detect the changes in species important from a conservation status FMBF point of view, the diagnostic species for beech forests in the phytosociological system of plant communities (diagnostic species of alliance *Fagion sylvaticae* and association *Dentario glandulosae Fagetum*, [48]) that underlie the Habitat Directive for the Natura 2000 program sites in the EU were taken into account. In this case, we studied the temporal trend in the occurrence of these species.

Differences between the scores obtained based on three vegetation censuses were tested using several sample repeated measures ANOVA or Friedman tests with posteriori Tukey's or Wilcoxon's tests with Bonferroni correction, respectively. ANOVA test was used when the data met the assumption of normality. Otherwise, the Friedman test was used. To reveal dependencies between changes in the stand structure, as well as the intensity of forest management and diversity indices and groups of species, the Spearman's rank correlation test was applied. Unless stated otherwise, statistical significance was estimated for $p \leq 0.05$.

To avoid the overestimation of common species of high abundance, and to improve the normality of distribution, before statistical analyses, all data were square root-transformed. In order to avoid errors resulting from the differences in herb layer compositions due to shifts in the spring season (in response to global change), early spring herbaceous species were excluded from the analyses. In order to avoid errors resulting from the incorrect identification of similar species, ferns of the genus *Dryopteris* were combined into one group. The same applied to *Senecio fuchsii* and *S. nemorensis*.

All statistical analyses were calculated using the PAST software package 4.0 (Hammer et al. [49]).

3. Results

3.1. Dynamics of Change in the Forest Structure and Intensity of Forest Management

The stand age increased from the first to the third census. In both study periods, the tree layer cover decreased and shrub layer cover increased. However, only in the second study period were these changes statistically significant. The highest average tree height was noted during the second census. However, this was not significantly different from the tree height noted during the first census, and both were statistically higher than the average tree height in the third census. The average DBH statistically increased in the first study period and decreased in the second. Species richness of the tree layer showed an increase, and species richness of the shrub layer decreased from the first to third censuses (Table 2).

Table 2. Mean (±SE) values of forest structure characteristics in three subsequent vegetation censuses. Differences between vegetation censuses were tested by several sample repeated measures tests. Depending on normality distribution, an ANOVA or Friedman test was used. Values with different superscript letters differed significantly based on Tukey's or Wilcoxon's posteriori tests at the *p* level, at least $p \leq 0.05$. Intensity of forest management treatments were ranked on a five-point scale as follows: no interference—1, thinning—4, irregular shelterwood treatments lasting 10 years—6, irregular shelterwood treatments lasting 20 years—7, and regular shelterwood treatments—9 (for details, please refer to the Materials and Methods section). F and Chi^2—ANOVA and Friedman test score, respectively.

	Test Score	**Mean (±SE) Values**		
	F, ^{x} Chi^2	**1970s**	**2000s**	**2010s**
Cover of tree layer (%)	^{x}6.7 *	87.3 (1.02) ^{a}	84.0 (1.16) ^{a}	77.6 (2.60) ^{b}
Cover of shrub layer (%)	^{x}40.0 ***	5.6 (0.63) ^{a}	8.8 (1.45) ^{a}	27.2 (2.77) ^{b}
Average tree height (m)	^{x}11.1 **	30.3 (0.47) ^{a}	31.0 (0.55) ^{a}	27.1 (0.73) ^{b}
Average DBH (cm)	6.3 **	37.9 (1.43) ^{a}	49.0 (3.51) ^{b}	40.1 (2.35) ^{a}
Tree layer species richness (No. of species)	^{x}27.5 ***	2.9 (0.15) ^{a}	2.3 (0.11) ^{b}	1.8 (0.08) ^{c}
Shrub layer species richness (No. of species)	3.5 *	1.7 (0.11) ^{a}	2.3 (0.17) ^{ab}	2.3 (0.15) ^{b}
Age of stands (year)	74.0 ***	85.3 (2.45) ^{a}	96.3 (2.50) ^{b}	113.0 (2.49) ^{c}
Intensity of forest management (ranks)	5.3 **	6.5 (0.31) ^{a}	5.4 (0.28) ^{b}	5.7 (0.25) ^{ab}

* $p \leq 0.05$. ** $p \leq 0.01$. *** $p \leq 0.001$.

Between the 1970s, and 2000s, we observed significant changes in the intensity of forest management. In the 1970s, over 45% of sampling plots were located in stands without or under small forest management pressure. However, at the same time, a similar percentage of sampling plots were located in stands subject to severe forest management treatments. In the 2000s, the severity of forest management decreased due to the replacement of regular shelterwood treatments to irregular shelterwood treatments. In the 2010s, most stands achieved the rotation age. As a result, there was a substantial decrease in the number of sampling plots with stands without or under small forest management pressure. At the same time, the number of sampling plots with stands subject to long-term, irregular shelterwood treatments with clearly visible stand renewal processes increased (Table 2 and Figures 2 and 3).

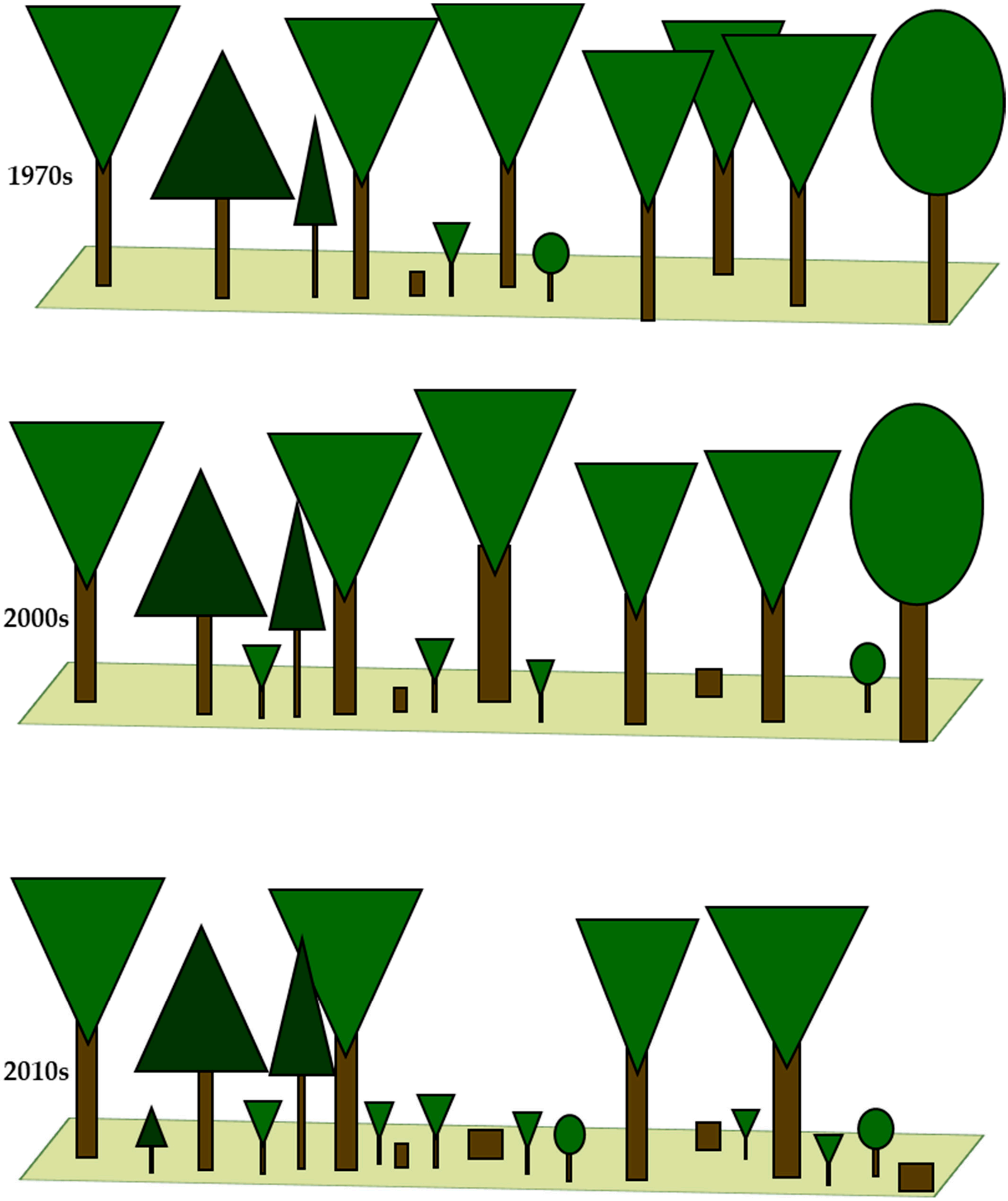

Figure 2. Schematic representation of the vertical and horizontal structures of fertile mountain beech forests in the 1970s, 2000s, and 2010s.

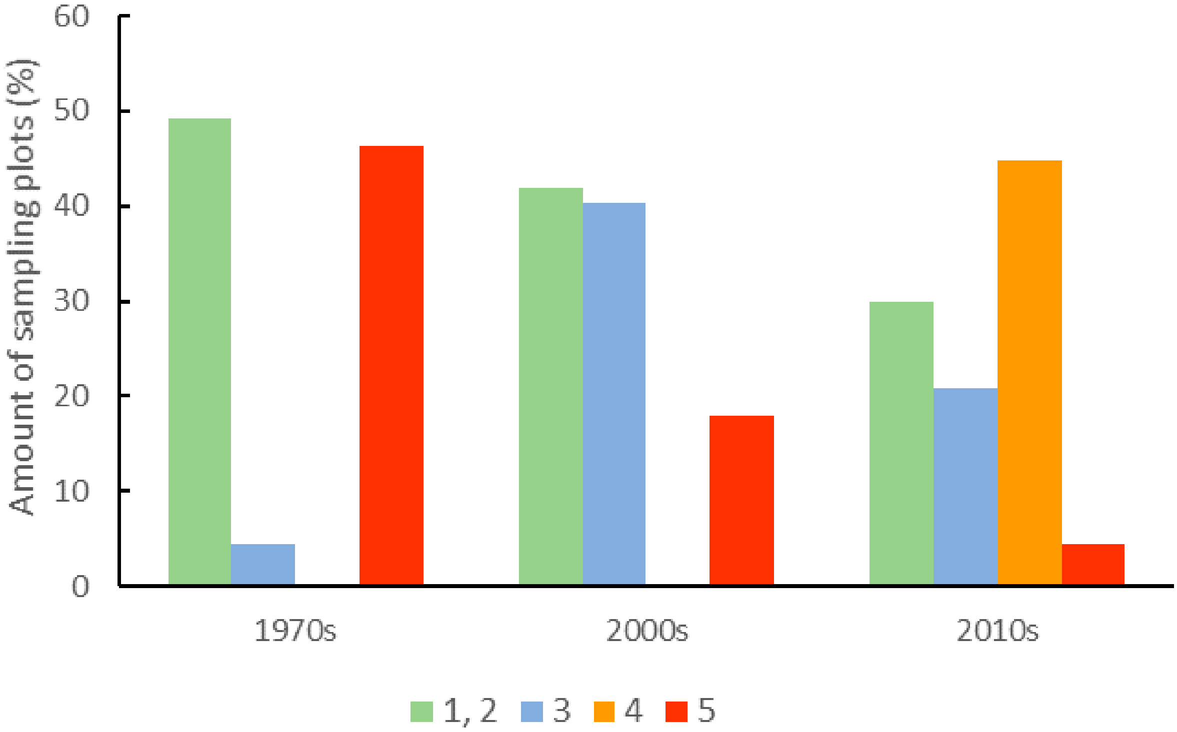

Figure 3. Forest management treatments on sampling plots in the three subsequent vegetation censuses. 1—no interference, 2—thinning, 3—irregular shelterwood treatments lasting 10 years, 4—irregular shelterwood treatments lasting 20 years, and 5—regular shelterwood treatments.

3.2. Dynamics of Change in the Herbaceous Plant Diversity Metrics

The highest gamma diversity, defined as the total species pool noted during each of the censuses, was recorded in the 2000s (131 species). The total pool of species in the 1970s and 2010 was similar and amounted to 117 and 118 species, respectively.

Shannon diversity index was highest in the 2000s and lowest in the 2010s. The evenness index was lowest in the 2000s and highest in the 2010s (Figure 4). Several sample repeated measures tests confirmed a decrease in the Shannon diversity (ANOVA test: F = 13.4, $p \leq 0.001$) and in the variation in species abundance on the sampling plots in the 2010s (increase in the evenness index, Friedman test: $\text{chi}^2 = 54.6$, $p \leq 0.001$).

Beta diversity expressed by the Sorensen and Simpson dissimilarity indices was highest in the 2010s and lowest in the 2000s. Statistical tests confirmed decreased beta diversity indices at the end of the first study period and an increase at the end of the study period (Sorensen: F = 47.1, $p \leq 0.001$; Simpson: F = 50.3, $p \leq 0.001$). Beta diversity expressed by the nestedness index, systematically decreased from the 1970s. In the 2010s, it was statistically lower than in the 1970s (F = 3.7, $p \leq 0.05$) (Figure 4).

Changes in the beta diversity indices indicated homogenization in species composition during the first study period, with a significant decrease in species replacement between sampling plots. During the second period, there was a clear differentiation in species composition, with a significant increase in species replacement between sampling plots. Moreover, the comparison of beta diversity between the 1970s and the 2010s showed the differentiation process with a significant increase in species replacement and a simultaneous decrease in the nestedness beta diversity component (Figure 4).

The forest habitat heterogeneity between plots increased during the 40 years of the study (the M-H dissimilarity index based on data from three subsequent censuses were: 0.0014, 0.0022, and 0.0033). Several sample repeated measures ANOVA tests showed significant differences between these indices (F = 16.9, $p \leq 0.001$), and the posteriori Tukey's test confirmed a significantly higher forest habitat heterogeneity in the 2010s than in the 1970s and 2000s. These results indicated that the habitat heterogeneity increased during the second study period. We found a strong correlation between $\Delta\alpha_{\mathrm{Sha}}$ and $\Delta\beta_{\mathrm{Sor}}$ indices and the changes in the habitat heterogeneity (negative, $r_s = -0.48$, $p \leq 0.001$; positive, $r_s = 0.47$, $p \leq 0.001$, respectively).

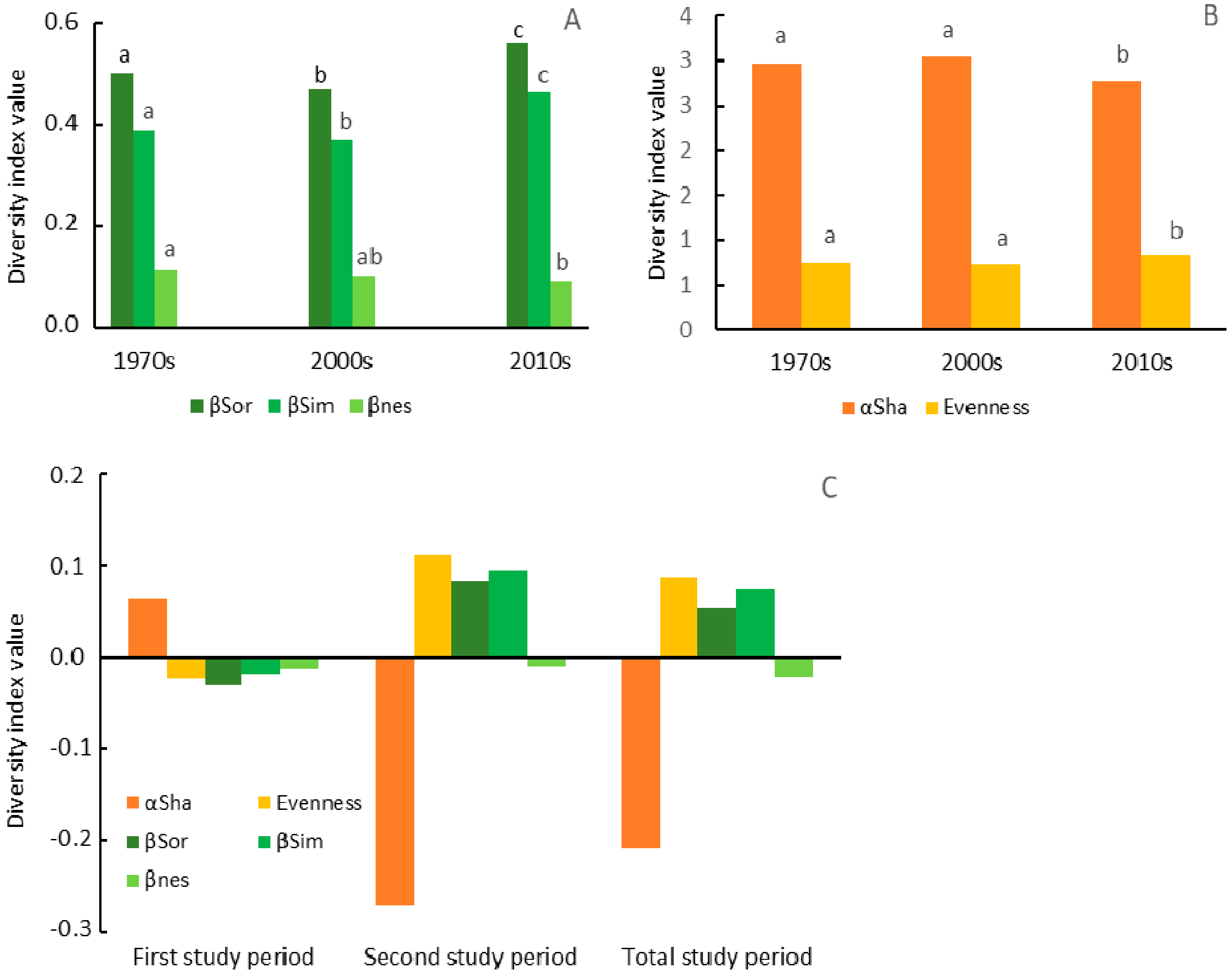

Figure 4. Mean values of the alfa and beta diversity indices in the three subsequent vegetation censuses. (**A**) A pairwise β_{Sor} dissimilarity index partitioned into the β_{Sim} (replacement) and β_{nes} (nestedness) components. (**B**) Alfa diversity indices. (**C**) Changes in the alfa and beta diversity indices during the first, second, and total study periods.

At the community level, the mean frequency of species occurrence was highest in the 2000s, intermediate in the 1970s, and lowest in the 2010s. Based on the statistical results, the frequency of species occurrence from the 2010s was significantly lower than in earlier censuses. At the plot level, the mean species richness was highest in the 2000s, intermediate in the 1970s, and lowest in the 2010s. The total species abundance was lowest in the 1970s and highest in the 2010s. The statistical results indicated a decrease of species richness and an increase of total species abundance in the 2010s (Table 3 and Figure 5). In the case of the ecological groups of species defined based on the Ellenberg indicator values, we found the highest species richness of groups: L_L, T_L, F_H, R_H, and N_H in the 2000s and lowest in the 2010s. Vegetation censuses differed significantly in the richness of shade-tolerant and moisture-demanding species. The richness of the species, which preferred soil with higher pH and rich in nutrients, as well as cooler habitats, significantly decreased in the 2010s (Table 3).

Table 3. Mean (±SE) values of herbaceous layer characteristics in three subsequent vegetation censuses. Differences between vegetation censuses were tested by several sample repeated measures tests. Depending on the normality distribution, an ANOVA or Friedman test was used. Values with different superscript letters (a,b,c) differed significantly based on Tukey's or Wilcoxon's posteriori tests at the p level, at least $p \leq 0.05$. F and Chi^2—ANOVA and Friedman test scores, respectively. L, T, F, R, and N: Ellenberg indicator values for light, temperature, moisture, reaction, and nitrogen. The L and H subscripts indicate low and high indicator values, respectively.

	Test Score	**Mean (±SE) Values**		
	F, ^{x}Chi^2	**1970s**	**2000s**	**2010s**
Frequency of species occurrence	^{x}23.2 ***	16.0 (±1.8) ^{a}	17.4 (±1.9) ^{a}	11.5 (±1.5) ^{b}
Species richness (No. of species)	42.5 ***	27.9 (±1.0) ^{a}	30.2 (±1.0) ^{a}	20.1 (±0.7) ^{b}
Total abundance of species (%)	^{x}26.5 ***	86.2 (±4.5) ^{a}	98.1 (±3.8) ^{a}	128.7 (±6.8) ^{b}
Number of species with high or low habitat requirements				
L_L	56.2 ***	8.9 (±0.3) ^{a}	10.1 (±0.3) ^{b}	6.2 (±0.3) ^{c}
L_H	2.7	2.4 (±0.2) ^{a}	2.8 (±0.2) ^{a}	2.7 (±0.2) ^{a}
T_L	^{x}27.1 ***	2.1 (±0.2) ^{a}	2.4 (±0.2) ^{a}	1.4 (±0.1) ^{b}
T_H	2.3	1.6 (±0.2) ^{a}	1.9 (±0.2) ^{a}	1.6 (±0.2) ^{a}
F_H	^{x}32.6 ***	2.7 (±0.2) ^{a}	3.8 (±0.2) ^{b}	1.8 (±0.2) ^{c}
R_L	^{x}1.8	0.2 (±0.1) ^{a}	0.4 (±0.1) ^{a}	0.3 (±0.1) ^{a}
R_H	25.2 ***	10.4 (± 0.5) ^{a}	10.5 (±0.5) ^{a}	7.0 (±0.4) ^{b}
N_L	0.6	0.4 (±0.1) ^{a}	0.4 (±0.1) ^{a}	0.3 (±0.1) ^{a}
N_H	19.5 ***	9.7 (±0.5) ^{a}	10.7 (±0.6) ^{a}	7.0 (±0.4) ^{b}

*** $p \leq 0.001$.

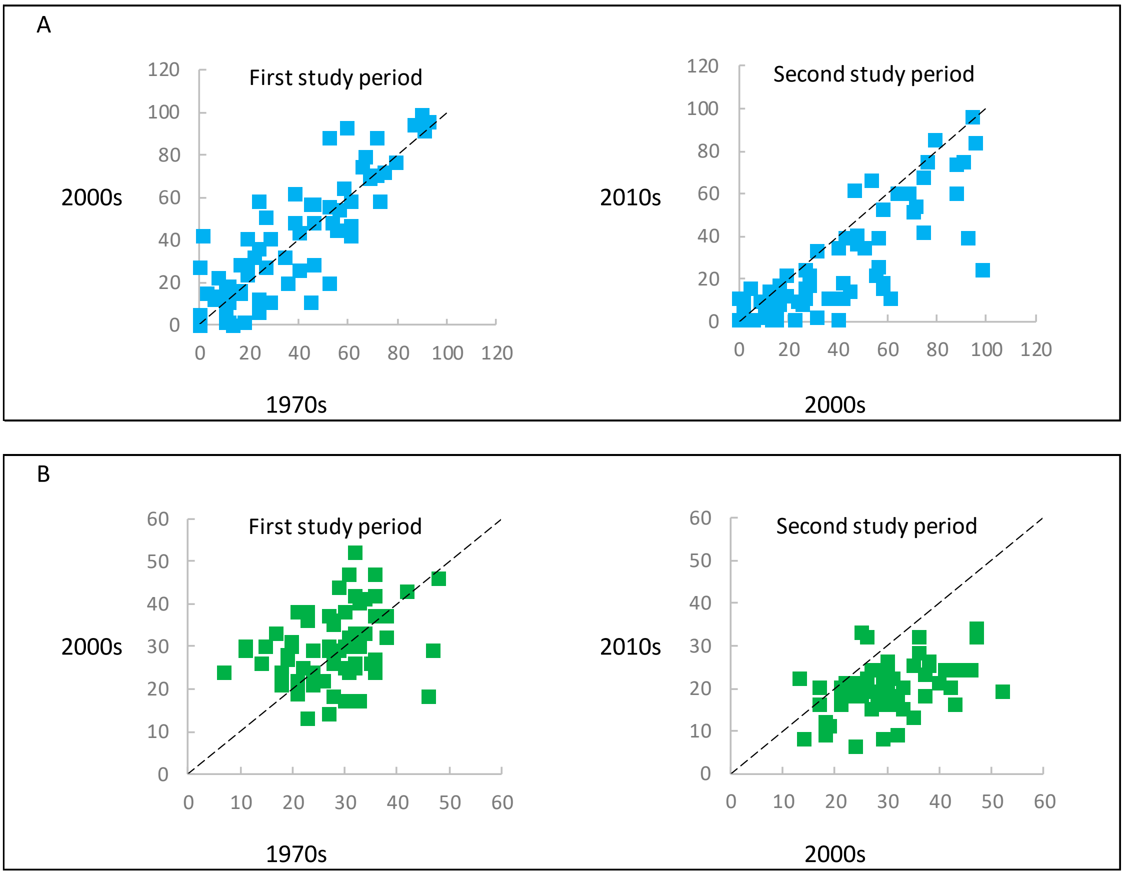

Figure 5. Frequency of species occurrence (**A**), and species richness (**B**) on the sampling plots during the vegetation censuses. For the sake of clarity, diagram A was plotted from species with a frequency of occurrence of at least 10% over any vegetation census. The dashed lines presents a hypothetical situation where the frequency of species occurrence or species richness in the sampling plots were equal between the vegetation censuses.

From the pool of 20 winner species, 16 and 19 species noted changes, respectively, during the first and second study periods. Among them, the highest increase was noted by disturbance-related species with higher light requirements: *Rubus hirtus* and ferns from genus *Dryopteris*. At the same time, from the pool of 45 loser species, a similar number of species noted changes (41 and 42 species), respectively, during the first and second study periods. Among them, the highest decrease was noted for typical, shade-tolerant FMBF species: *Actaea spicata*, *Athyrium filix-femina*, *Daphne mezereum*, *Mercurialis perennis*, *Oxalis acetosella*, and *Polygonatum multiflorum*. Moreover, a large group of diagnostic species of FMBF was found among the loser species: *Dentaria glandulosa*, *D. bulbifera*, *Symphytum cordatum*, *S. tuberosum*, *Euphorbia amygdaloides*, and *Glechoma hirsuta*. Additionally, we found a group of species that decreased in frequency of occurrence and increased in abundance between 1970s and 2010s, e.g., *Galeobdolon luteum* and *Fagus sylvatica* (Table S1).

Between the 1970s and 2000s, only a slight increase in the occurrences of species important from a conservation status of the FMBF viewpoint was found (from 307 to 322 occurrences). The change of the management system, as well as the intensification of forest management, along with the increase in the age of the forest, resulted in a decrease in the occurrence of diagnostic species of FMBF between the 2000s and 2010s (from 322 to 253 occurrences).

3.3. Impact of Changes in the Forest Structure, as Well as Intensity of Forest Management on the Herbaceous Plant Diversity Metrics

We did not find dependencies between the changes in the forest characteristics and changes in the herbaceous plant diversity metrics during the first study period.

During the second study period, the herbaceous plant alpha diversity metrics showed a decrease, with an increase in shrub layer cover. The total herbaceous plant beta diversity (β_{Sor}) increased with a decrease in the height and number of tree species. Components of the total beta diversity (β_{Sim} and β_{nes}) revealed additional, inverse dependency from the cover of the tree layer (Tables 2 and 4). The changes in the forest structure during the second study period were much greater than in the first period (Table 4). A decrease in the tree layer cover and tree height and increase in the shrub layer cover indicate the intensive felling of old trees and replacement with a new tree generation during the second study period. Therefore, the described-above relationship between the changes in the forest structure and herbaceous plant diversity metrics was attributed to the higher intensity of management treatment in the 2010s.

Table 4. Correlation between changes in the forest structure characteristics and changes in the herbaceous plant diversity metrics, expressed by Spearman's correlation coefficients. The correlation coefficients at the p level, at least $p \leq 0.05$, have been highlighted in grey and italicized. In the case of groups of species with high and low habitat requirements, the groups that recorded significant differences in the species richness between the vegetation censuses (according to the results provided in Table 3) were selected for correlation.

	Δ Cover of Tree Layer (%)	**Δ Cover of Shrub Layer (%)**	**Δ Average Tree Height (m)**	**Δ Average DBH (cm)**	**Δ Tree Layer Species Richness (No. of Species)**	**Δ Shrub Layer Species Richness (No. of Species)**	**Δ Age of Stands (Year)**
First study period							
$\Delta\alpha_{Sha}$	0.08	−0.21	0.06	−0.03	0.19	0.04	0.05
ΔEvenness	0.12	−0.01	−0.05	−0.2	0.1	−0.15	−0.05
ΔL_L	0.21	−0.17	0.05	−0.18	0.1	0.03	−0.09
ΔT_L	−0.07	−0.19	0.04	0.07	0.02	−0.04	0.07
ΔF_H	−0.13	−0.17	0.06	0.12	0.18	0.02	0.17
ΔR_H	−0.03	−0.16	0.08	0.04	0.04	0.09	0,00
ΔN_H	−0.06	−0.15	0.01	0,00	0.09	0.12	−0.04
ΔSpecies richness	0.02	−0.19	0.05	−0.02	0.15	0.11	0.01
$\Delta\beta_{Sor}$	0,00	0.15	−0.18	−0.06	−0.14	−0.08	−0.06
$\Delta\beta_{Sim}$	−0.02	0.07	0,00	0,00	−0.02	0.04	0.04
$\Delta\beta_{nes}$	0.04	0.03	−0.14	0.06	−0.08	−0.07	−0.09

Table 4. *Cont.*

	Δ Cover of Tree Layer (%)	**Δ Cover of Shrub Layer (%)**	**Δ Average Tree Height (m)**	**Δ Average DBH (cm)**	**Δ Tree Layer Species Richness (No. of Species)**	**Δ Shrub Layer Species Richness (No. of Species)**	**Δ Age of Stands (Year)**
Second study period							
$\Delta\alpha_{Sha}$	−0.05	*−0.26*	0.18	−0.06	0.03	0.05	−0.07
ΔEvenness	−0.03	−0.07	−0.01	−0.17	−0.12	*−0.26*	−0.2
ΔL_L	0.2	*−0.3*	−0.08	−0.23	0.07	−0.09	0,00
ΔT_L	−0.12	−0.05	0.19	0.03	0.03	0.06	−0.07
ΔF_H	−0.09	*−0.3*	0.08	−0.08	0.14	0.13	−0.18
ΔR_H	0.04	*−0.35*	0.09	−0.06	0.18	0.12	−0.03
ΔN_H	0.07	*−0.4*	0.07	−0.1	0.15	0.14	−0.04
ΔSpecies richness	0.02	*−0.37*	0.18	−0.11	0.17	0.08	−0.07
$\Delta\beta_{Sor}$	−0.08	0.04	*−0.25*	0.02	*−0.26*	−0.13	0.05
$\Delta\beta_{Sim}$	*−0.3*	0.01	−0.08	0.21	−0.24	0.12	0.11
$\Delta\beta_{nes}$	*0.27*	0.04	0.02	−0.1	0.05	*−0.24*	−0.07

4. Discussion

Based on the stand age and the characteristics of the forest structure, we can define the forest developmental stages that dominated during the three subsequent vegetation censuses. The stand age exceeding 85 years on average, DBH over 30 cm, and the lack of differences between most features of the forest structure from the 1970s and the 2000s indicate the dominance of the optimum forest developmental stage during the first and second vegetation census. [12]. However, the greater DBH of trees, as well as the lower species richness of stands with the simultaneously growing species richness of the shrub layer point to the fact that the stands from the 2000s were dominated by the late optimum stage. The forests from the 2010s were very different compared to those in the 1970s and 2000s. Decline in tree size (height and DBH), tree layer cover, and species richness, with the simultaneous increase in the coverage of the intermediate forest layer (consisting of tree saplings and shrubs), led to the assumption that in the 2010s the terminal stage was dominant [12].

We found that the within-plot and between-plot herbaceous plant diversity metrics showed inconsistent patterns alongside changes in the beech forest structure, management system, and intensity of the forest management during the last 40 years. Our results disclose that change of the dominant developmental stage of the forest from the optimum to late-optimum stage, combined with a change in the management system to a less-invasive, closer-to-nature at the beginning causes an increase in within-plot and a decrease in between-plot herbaceous plant diversity. However, in the following years (2010s, development of terminal stage), when the intensity of forest management combined with forest renewal processes increased, the within-plot herbaceous plant diversity strongly decreased, and the between-plot increased, except for beta nestedness, which decreased. We argued that this increase in beta diversity can be misleading when assessing the status of the forest diversity or planning conservation actions because of a decrease in the alpha diversity metrics, as well as including diagnostic species of beech forests. This loss of species is in accordance with the "area heterogeneity trade-off hypothesis" [36] and results in a slight decline in the diversity on the regional level (gamma diversity) in the 2010s.

4.1. Dynamics of Change in the Herbaceous Plant Diversity Metrics

The alpha diversity (α_{Sha}, within-plot diversity) only slightly increased during the first study period and substantially decreased in the second period. At the same time, changes in the beta diversity (β_{Sor}, as well as β_{Sim}, between-plot diversity) between subsequent vegetation censuses were statistically significant, showing a clear nonlinear, U-shaped pattern of changes. Inconsistency between the revealed patterns of herbaceous plant diversity indicates that alpha and beta diversity react inversely to changes of forest management treatments and/or the severity of the forest management system. Moreover, beta diversity is more sensitive to these changes. Opposite patterns of alpha and beta diversity changes can be explained by the inherent relationships between most of the traditional alpha and beta diversity indices [50]. However, we did not find the same clear U-shaped trend in alpha diversity, as was in the case of the beta diversity. This means that alpha diversity reacts to a lesser extent than beta diversity to a decrease in the intensity of forest management treatments. Nevertheless, both alpha and beta diversity react strongly to increases in forest management treatments (decrease in alpha and increase in beta diversity metrics). There are two possible explanations for the decline in alpha diversity measures. The first is derived from "area heterogeneity trade-off hypothesis" [36]. We found significantly higher habitat heterogeneity during the third vegetation census than in the past. According to the aforementioned hypothesis, this increase in habitat heterogeneity could decrease the resource availability and increase the local extinction of the species, especially those associated with typical beech forest habitats. Furthermore, it could have been caused by the reduction of the total abundance of some species across the communities and, consequently, their rarer occurrence under the influence of high-intensity forest use [51].

Since the findings on long-term changes in the diversity of herbaceous forest plants are most often based on a comparison of vegetation records from two censuses, they can only show an increase, a decrease, or no change between records. To reliably recognize the patterns of plant diversity dynamics, a time series of vegetation data recorded on permanent sampling plots are needed [23]. Our research showed that over 40 years, alpha diversity decreased, and the total beta diversity increased. However, this pattern of changes was consistent with the course of changes in the second study period (between the 2000s and 2010s). At the same time, it was significantly different from the pattern of changes recorded in the first, three times longer study period (30 years between the 1970s and 2000s). Thus, our results indicated that the temporal changes in diversity detected by comparing the records from the two censuses may (1) hide the actual course of the changes and/or (2) contribute to the misinterpretation of the trend of long-term changes in the herbaceous plant diversity and, consequently, lead to the incorrect assessment of the state of forest diversity or conservation action plans (Figure 6). This is well-evidenced by the contrast between an increase in beta diversity and the decline in the share of diagnostic species of herbaceous vegetation of FMBF. The occurrence of a diagnostic species depends on the degree of conservation of habitat conditions, typical for a well-preserved community. Hence, the decline of diagnostic species for beech forests indicates the decay of habitats typical of well-preserved FMBF. It is an open question that requires further research, whether the disappearance of these species is related exclusively to the final developmental stage of the managed forest (terminal stage) or whether it is of a permanent, irreversible nature (independent of developmental stage). Thus, our results confirm the great importance of conservation-relevant species as an important metric of the conservation status of forests [11].

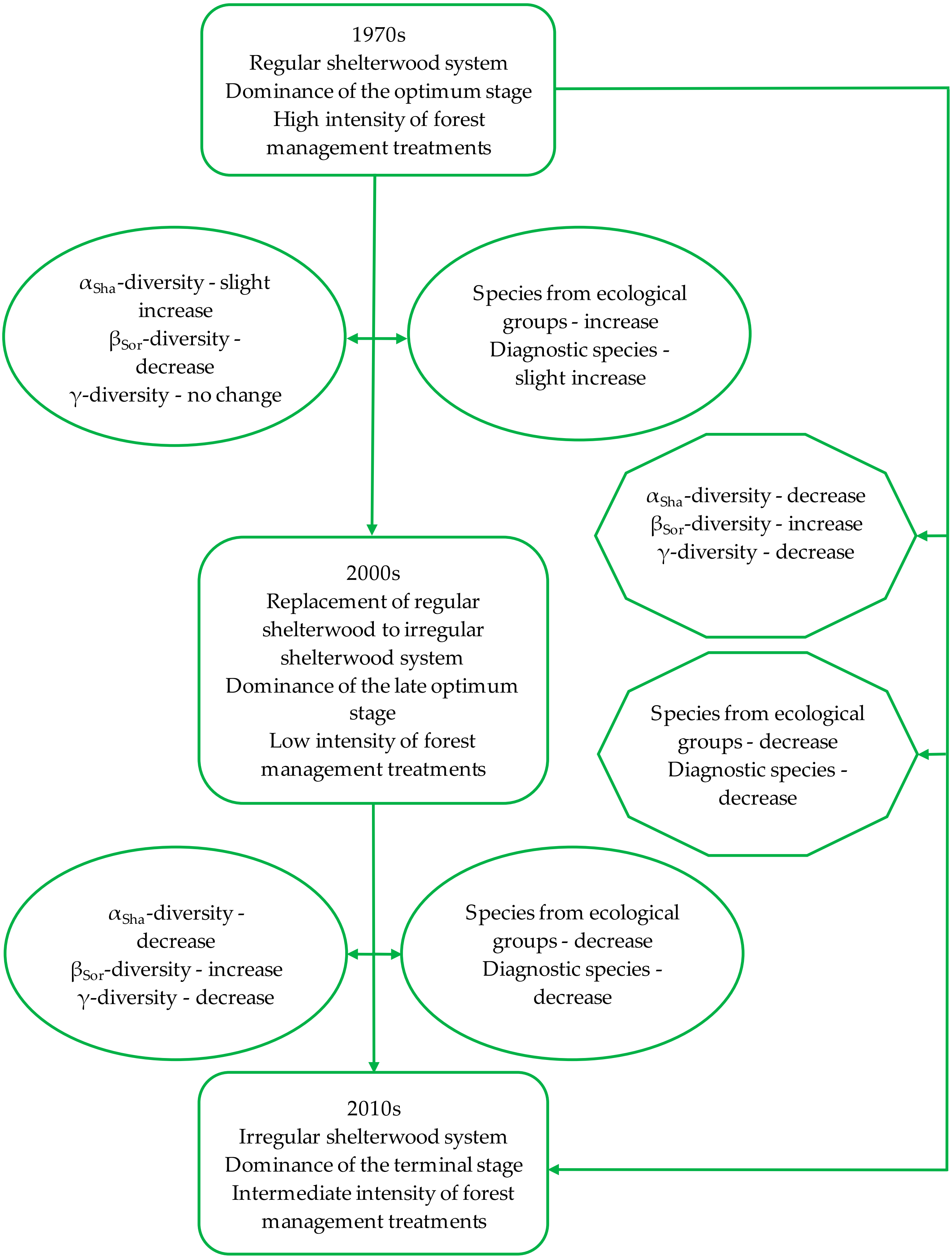

Figure 6. Impact of the forest management and stand structure on the herbaceous plant diversity in Carpathian beech forests with over 40 years of forest development—comparison of the results obtained on the basis of records from three and two time points.

4.2. Impact of Changes in Forest Structure as Well Intensity of Forest Management on Herbaceous Plant Diversity Metrics

During the first study period, the age of the forest increased, and the regular shelterwood was replaced by closer-to-nature, irregular shelterwood. As a result of the aging of the forest, the species richness of the stand decreased, and the DBH (and DBH variability) increased. Additionally, the changes of the management system resulted in a decrease in intensity of the forest management treatment. At the same time, diversity metrics of herbaceous plants slightly increased within-plots and significantly decreased between-plots. In the second study period, along with the growing age of the stands, there were significant changes in the structure of the tree and shrub layers. Moreover, because of the change of the dominant stage of the stand development from the optimum to terminal, the intensity of the forest management treatments increased. At the same time, the diversity metrics of the herbaceous layer significantly decreased within-plots and increased between-plots.

We argue, similarly to Dieler et al. [9] and Hilmers et al. [10], that the revealed pattern of diversity was a response to complex changes in the forest management affecting the forest structure and development status. The results obtained by Schall et al. [13] suggest a negative impact of the closer-to-nature management system on the spatial diversity of the forest habitats and, thus, on beta diversity. Indeed, after replacing the regular with an irregular shelterwood system (first study period), we found a decline in beta diversity (between-plot diversity). However, we did not find significant changes in the habitat heterogeneity, nor with the alpha diversity (within-plot diversity). Moreover, we did not find a lower beta diversity in forests managed by the closer-to-nature management system during the second study period; in fact, it was higher (except beta nestedness). At the end of the second study period, the habitat heterogeneity was also greater, however, this did not result in an increase in the alpha diversity, which decreased significantly due to the high density of tree regeneration (in this work, represented by the shrub layer). This means that the introduction of a closer-to-nature management system did not result in decreased heterogeneity of the habitats and herbaceous plant beta diversity. We argue that this was the result of intensified renewal processes taking place in the terminal stage of stands development, which increased the forest habitat heterogeneity. At the same time, the intensive forest management related to tree removal and the development of new tree generation caused the decline in alpha diversity metrics. This decline in alpha diversity enhanced the effect of increased beta diversity. Thus, recorded during a 40-year time period, the increase in beta diversity can be strongly misleading from the point of view of the forest conservation status assessment.

5. Conclusions

Our results showed that the herbaceous plant diversity is highly dependent not only on the forest management system but, also, on the intensity of forest treatments [13]. We showed the importance of temporal interactions between the changes in the management system—the dominant development stage—the intensity of the forest treatments, and the herbaceous plant diversity. Hence, it should be assumed that different levels of intensity of these interactions will result in different patterns of change in herbaceous plant diversity. In view of the complexity of the processes affecting the herbaceous plant diversity in FMBF, it would be a mistake to reject or prioritize alpha or beta diversity measurements to determine the diversity dynamics or assess the conservation status of these forests. We argue that, in order to reveal the real course of long-term changes in herbaceous plant diversity and to properly assess the state of forest biodiversity as well as conservation status or action plans, we need to learn more about the long-term interactions between drivers that control the forest structure and the various measures of plant diversity.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/biology10050406/s1, Table S1: Herbaceous species with more than 10% changes in frequency of occurrence and/or significant changes in abundance. Increases in frequency of occurrence and/or abundance of species are marked in bold and decreases by underlining. L, T, F, R, N: Ellenberg's indicator values for light, temperature, moisture, reaction and nitrogen.

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References

1. Gilliam, F.S. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* **2007**, *57*, 845–858. [CrossRef]
2. Rackham, O. Ancient woodlands: Modern threats. *New Phytol.* **2008**, *180*, 571–586. [CrossRef]
3. Bengtsson, J.; Nilsson, S.G.; Franc, A.; Menozzi, P. Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manag.* **2000**, *132*, 39–50. [CrossRef]
4. Perring, M.P.; Bernhardt-Römermann, M.; Baeten, L.; Midolo, G.; Blondeel, H.; Depauw, L.; Landuyt, D.; Maes, S.L.; De Lombaerde, E.; Carón, M.M.; et al. Global environmental change effects on plant community composition trajectories depend upon management legacies. *Glob. Chang. Biol.* **2018**, *24*, 1722–1740. [CrossRef] [PubMed]
5. Bürgi, M.; Li, L.; Kizos, T. Exploring links between culture and biodiversity: Studying land use intensity from the plot to the landscape level. *Biodivers. Conserv.* **2015**, *24*, 3285–3303. [CrossRef]
6. Franklin, J.; Serra-Diaz, J.; Syphard, A.; Regan, H. Global change and terrestrial plant community dynamics. *Proc. Nat. Acad. Sci. USA* **2016**, *113*, 3725–3734. [CrossRef] [PubMed]
7. Naaf, T.; Wulf, M. Habitat specialists and generalists drive homogenization and differentiation of temperate forest plant communities at the regional scale. *Biodivers. Conserv.* **2010**, *143*, 848–855. [CrossRef]
8. Kopecký, M.; Hédl, R.; Szabó, P. Non-random extinctions dominate plant community changes in abandoned coppices. *J. Appl. Ecol.* **2013**, *50*, 79–87. [CrossRef]
9. Dieler, J.; Uhl, E.; Biber, P.; Müller, J.; Rötzer, T.; Pretzsch, H. Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. *J. For. Res.* **2017**, *136*, 739–766. [CrossRef]
10. Hilmers, T.; Friess, N.; Bässler, C.; Heurich, M.; Brandl, R.; Pretzsch, H.; Seidl, R.; Müller, J. Biodiversity along temperate forest succession. *J. Appl. Ecol.* **2018**, *5*, 2756–2766. [CrossRef]
11. Lelli, C.; Bruun, H.H.; Chiaruccia, A.; Donatia, D.; Frascarolia, F.; Fritz, O.; Goldberg, I.; Nascimbene, J.; Tøttrup, A.; Rahbek, C.; et al. Biodiversity response to forest structure and management: Comparing species richness, conservation relevant species and functional diversity as metrics in forest conservation. *For. Ecol. Manag.* **2019**, *432*, 707–717. [CrossRef]
12. Durak, T.; Bugno-Pogoda, A.; Durak, R. Application of forest inventories to assess the forest developmental stages on plots dedicated to long-term vegetation studies. *For. Ecol. Manag.* **2021**, *489*, 119041. [CrossRef]
13. Schall, P.; Gossner, M.M.; Heinrichs, S.; Fischer, M.; Boch, S.; Prati, D.; Jung, K.; Baumgartner, V.; Blaser, S.; Böhm, S.; et al. The impact of even-aged and uneven-aged forest management on regional biodiversity of multiple taxa in European beech forests. *J. Appl. Ecol.* **2018**, *55*, 267–278. [CrossRef]
14. Decocq, G.; Aubert, M.; Dupont, F.; Alard, D.; Saguez, R.; Wattez-Franger, A.; de Foucault, B.; Delelis-Dusollier, A.; Bardat, J. Plant diversity in a managed temperate deciduous forest: Understorey response to two silvicultural systems. *J. Appl. Ecol.* **2004**, *41*, 1065–1079. [CrossRef]
15. Ciancio, O.; Corona, P.; Lamonaca, A.; Portoghesi, L.; Travaglini, D. Conversion of clearcut beech coppices into high forests with continuous cover: A case study in central Italy. *For. Ecol. Manag.* **2006**, *224*, 235–240. [CrossRef]

16. Puettmann, K.J.; Wilson, S.M.; Baker, S.C.; Donoso, P.J.; Drössler, L.; Amente, G.; Harvey, B.D.; Knoke, T.; Lu, Y.; Nocentini, S.; et al. Silvicultural alternatives to conventional even-aged forest management—what limits global adoption? *For. Ecosyst.* **2015**, *2*, 1–16. [CrossRef]
17. O'Hara, K.L. What is close-to-nature silviculture in a changing world? *Forestry* **2016**, *89*, 1–6. [CrossRef]
18. Decocq, G.; Aubert, M.; Dupont, F.; Bardat, J.; Wattez-Franger, A.; Saguez, R.; de Foucault, B.; Alard, D.; Delelis-Dusollier, A. Silviculture-driven vegetation change in a European temperate deciduous forest. *Ann. For. Sci.* **2005**, *62*, 313–323. [CrossRef]
19. Baeten, L.; Bauwens, B.; De Schrijver, A.; De Keersmaeker, L.; Van Calster, H.; Vandekerkhove, K.; Roelandt, B.; Beeckman, H.; Verheyen, K. Herb layer changes (1954–2000) related to the conversion of coppice-withstandards forest and soil acidification. *Appl. Veg. Sci.* **2009**, *12*, 187–197. [CrossRef]
20. Müllerová, J.; Hédl, R.; Szabó, P. Coppice abandonment and its implications for species diversity in forest vegetation. *For. Ecol. Manag.* **2015**, *343*, 88–100. [CrossRef]
21. Durak, T.; Holeksa, J. Biotic homogenisation and differentiation along a habitat gradient resulting from the ageing of manager beech stands. *For. Ecol. Manag.* **2015**, *351*, 47–56. [CrossRef]
22. FOREST EUROPE 2020: State of Europe's Forests 2020. Available online: https://foresteurope.org/wp-content/uploads/2016/08/SoEF_2020.pdf (accessed on 13 April 2021).
23. Bakker, J.P.; Olff, H.; Willems, J.H.; Zobel, M. Why do we need permanent plots in the study of long-term vegetation dynamics? *J. Veg. Sci.* **1996**, *7*, 147–156. [CrossRef]
24. De Lombaerde, E.; Verheyen, K.; Perring, M.P.; Bernhardt-Römermann, M.; Van Calster, H.; Brunet, J.; Chudomelová, M.; Decocq, G.; Diekmann, M.; Durak, T.; et al. Responses of competitive understorey species to spatial environmental gradients inaccurately explain temporal changes. *Basic Appl. Ecol.* **2018**, *30*, 52–64. [CrossRef]
25. Van Calster, H.; Baeten, L.; De Schrijver, A.; De Keersmaeker, L.; Rogister, J.E.; Verheyen, K.; Hermy, M. Management driven changes (1967–2005) in soil acidity and the understorey plant community following conversion of a coppice-with-standards forest. *For. Ecol. Manag.* **2007**, *241*, 258–271. [CrossRef]
26. Durak, T.; Durak, R. Vegetation changes in meso-and eutrophic submontane oak–hornbeam forests under long-term high forest management. *For. Ecol. Manag.* **2015**, *354*, 206–214. [CrossRef]
27. Heinrichs, S.; Schmidt, W. Biotic homogenization of herb layer composition between two contrasting beech forest communities on limestone over 50 years. *Appl. Veg. Sci.* **2017**, *20*, 271–281. [CrossRef]
28. Paillet, Y.; Bergès, L.; Hjaltén, J.; Ódor, P.; Avon, C.; Bernhardt-Römermann, M.; Bijlsma, R.J.; De Bruyn, L.; Fuhr, M.; Grandin, U.; et al. Biodiversity differences between managed and unmanaged forests: Meta analysis of species richness in Europe. *Conserv. Biol.* **2010**, *24*, 101–112. [CrossRef] [PubMed]
29. Chaudhary, A.; Burivalova, Z.; Koh, L.P.; Hellweg, S. Impact of forest management on species richness: Global meta-analysis and economic trade-offs. *Sci. Rep.* **2016**, *6*, 1–10. [CrossRef] [PubMed]
30. Gotelli, N.J.; Colwell, R.K. Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. *Ecol. Lett.* **2001**, *4*, 379–391. [CrossRef]
31. McKinney, M.L.; Lockwood, J.L. Biotic homogenization: A few winners replacing many losers in the next mass extinction. *Trends Ecol. Evol.* **1999**, *14*, 450–453. [CrossRef]
32. Olden, J.D.; Rooney, T.P. On defining and quantifying biotic homogenization. *Glob. Ecol. Biogeogr.* **2006**, *15*, 113–120. [CrossRef]
33. Whittaker, R.H. Evolution and measurement of species diversity. *Taxon* **1970**, *21*, 213–251. [CrossRef]
34. Loreau, M. Are communities saturated? On the relationship between α, β, and γ diversity. *Ecol. Lett.* **2000**, *3*, 73–76. [CrossRef]
35. Melo, A.S.; Fernando, T.; Rancel, L.V.B.; Diniz-Filho, J.A.F. Environmental drivers of beta-diversity patterns in New-World birds and mammals. *Ecography* **2009**, *32*, 226–236. [CrossRef]
36. Allouche, O.; Kalyuzhny, M.; Moreno-Rueda, G.; Pizarro, M.; Kadmon, R. Area-heterogeneity tradeoff and the diversity of ecological communities. *Proc. Nat. Acad. Sci. USA* **2012**, *109*, 17495–17500. [CrossRef]
37. Dzwonko, Z. Forest communities of the Gory Słonne Range (Polish Eastern Carpathians). *Fragm. Flor. Geobot.* **1977**, *23*, 161–200.
38. Skiba, S.; Drewnik, M. Soil map of the polish carpathian mountains. *Rocz. Bieszcz.* **2003**, *11*, 15–20.
39. Meteorological Data. Averages and Monthly Totals. Available online: https://meteomodel.pl/dane/srednie-miesieczne/?imgwid=349220690&par=tm&max_empty=2 (accessed on 16 March 2021).
40. Jaworski, A.; Kołodziej, Z. Beech (Fagus sylvatica L.) forest of a selection structure in the Bieszczady Mountains (southeastern Poland). *J. For. Sci.* **2004**, *50*, 301–312. [CrossRef]
41. Braun-Blanquet, J. *Pflanzensoziologie. Grundzüge der Vegetationskunde*; Springer-Verlag: Wien, Austria; New York, NY, USA, 1964.
42. Baselga, A. Partitioning the turnover and nestedness components of beta diversity. *Glob. Ecol. Biogeogr.* **2010**, *19*, 134–143. [CrossRef]
43. Rooney, T.P.; Wiegmann, S.M.; Rogers, D.A.; Waller, D.M. Biotic impoverishment and homogenization in unfragmented forest understory communities. *Conserv. Biol.* **2004**, *18*, 787–798. [CrossRef]
44. Durak, T.; Durak, R.; Węgrzyn, E.; Leniowski, K. The impact of changes in species richness and species replacement on patterns of taxonomic homogenization in the Carpathian forest ecosystems. *Forests* **2015**, *6*, 4391–4402. [CrossRef]
45. Olden, J.D.; Poff, N.L. Toward a mechanistic understanding and prediction of biotic homogenization. *Am. Nat.* **2003**, *162*, 442–460. [CrossRef]

46. Ellenberg, H.; Weber, H.E.; Düll, R.; Wirth, V.; Werner, W.; Paulissen, D. Zeigerwerte von pflanzen in Mitteleuropa. *Scr. Geobot.* **1992**, *18*, 1–248.
47. Horn, H.S. Measurement of overlap in comparative ecological studies. *Am. Nat.* **1966**, *100*, 419–424. [CrossRef]
48. Matuszkiewicz, W. *Przewodnik do Oznaczania Zbiorowisk Roślinnych Polski. [A Guide for the Identification of Polish Plant Communities]*; Wydawnictwo Naukowe PWN: Warszawa, Polska, 2001.
49. Hammer, O.; Harper, D.A.T.; Ryan, P.D. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **2001**, *4*, 1–9.
50. Jost, L. Partitioning diversity into independent alpha and beta components. *Ecology* **2007**, *88*, 2427–2439. [CrossRef] [PubMed]
51. Karp, D.S.; Rominger, A.J.; Zook, J.; Ranganathan, J.; Ehrlich, P.R.; Daily, G.C. Intensive agriculture erodes b-diversity at large scales. *Ecol. Lett.* **2012**, *15*, 963–970. [CrossRef] [PubMed]

Table S1. Herbaceous species with more than 10% changes in frequency of occurrence and/or significant changes in abundance. Increases in frequency of occurrence and/or abundance of species are marked in bold and decreases by underlining. L, T, F, R, N: Ellenberg's indicator values for light, temperature, moisture, reaction and nitrogen.

	Frequency of occurences (%)			Changes in frequency of occurence (%)			Total abundance (sum of the mid-point percentage cover values)			Changes in abundance (%)			Ellenberg indicator values (EIVs)				
	1970s	2000s	2010s	First study period	Second study period	Total study period	1970s	2000s	2010s	First study period	Second study period	Total study period	L	T	F	R	N
Winners																	
Acer platanoides	1.5	41.8	10.4	40.3	-31.3	**9.0**	0.5	16.5	16.0	16.0	-0.5	**15.5**	4	6	x	x	x
Anemone nemorosa	52.2	88.1	59.7	35.8	-28.4	**7.5**	212.5	519.0	336.0	336.5	-183.0	**123.5**	x	x	5	x	x
Carex sylvatica	26.9	50.7	34.3	23.9	-16.4	**7.5**	9.0	24.5	66.0	15.5	41.5	**57.0**	2	5	5	6	5
Dryopteris sp.	86.6	94.0	95.5	7.5	1.5	**9.0**	44.0	73.5	434.0	29.5	361.0	**390.5**	-	-	-	-	-
Impatiens parviflora	0.0	13.4	7.5	13.4	-6.0	**7.5**	0.0	9.5	24.5	9.5	15.0	**24.5**	4	6	5	x	6
Juncus effusus	0.0	1.5	10.4	1.5	9.0	**10.4**	0.0	0.5	25.5	0.5	25.0	**25.5**	8	5	7	3	4
Lysimachia nemorum	0.0	26.9	10.4	26.9	-16.4	**10.4**	0.0	11.5	25.5	11.5	14.0	**25.5**	2	5	7	7	7
Lysimachia vulgaris	0.0	0.0	9.0	0.0	9.0	**9.0**	0.0	0.0	25.0	0.0	25.0	**25.0**	6	x	8	x	x
Platanthera bifolia	0.0	0.0	7.5	0.0	7.5	**7.5**	0.0	0.0	5.0	0.0	5.0	**5.0**	6	x	5	7	x
Rubus hirtus	67.2	79.1	85.1	11.9	6.0	**17.9**	52.5	552.5	569.0	500.0	16.5	**516.5**	7	4	5	x	x
Rumex obtusifolius	0.0	4.5	14.9	4.5	10.4	**14.9**	0.0	1.5	17.5	1.5	16.0	**17.5**	7	5	6	x	9
Salvia glutinosa	56.7	53.7	65.7	-3.0	11.9	**9.0**	24.0	35.0	216.0	11.0	181.0	**192.0**	4	5	6	7	7
Anthriscus sylvestris	0.0	0.0	10.4	0.0	10.4	**10.4**	0.0	0.0	25.5	0.0	25.5	25.5	7	x	5	x	8
Acer pseudoplatanus	71.6	88.1	73.1	16.4	-14.9	1.5	29.0	110.5	230.0	81.5	119.5	**201.0**	4	x	6	x	7
Galium odoratum	79.1	76.1	74.6	-3.0	-1.5	-4.5	239.0	261.0	573.0	22.0	312.0	**334.0**	2	5	5	6	5
Hieracium murorum	0.0	0.0	6.0	0.0	6.0	6.0	0.0	0.0	7.0	0.0	7.0	**7.0**	-	-	-	-	-
Impatiens noli-tangere	58.2	64.2	59.7	6.0	-4.5	1.5	310.0	203.0	584.0	-107.0	381.0	**274.0**	4	5	7	7	6
Polystichum braunii	0.0	1.5	6.0	1.5	4.5	6.0	0.0	0.5	9.5	0.5	9.0	**9.5**	3	4	6	6	7
Senecio sp.	65.7	74.6	67.2	9.0	-7.5	1.5	24.5	32.5	146.0	8.0	113.5	**121.5**	7	-	-	x	8
Stellaria holostea	7.5	13.4	13.4	6.0	0.0	6.0	2.5	21.5	60.5	19.0	39.0	**58.0**	5	6	5	6	5
Veronica montana	23.9	58.2	17.9	34.3	-40.3	-6.0	13.0	19.5	33.5	6.5	14.0	**20.5**	4	5	7	5	6
Losers																	
Anthriscus nitida	22.4	31.3	1.5	9.0	-29.9	-20.9	7.5	27.5	3.0	20.0	-24.5	-4.5	4	4	6	8	8
Arum alpinum	10.4	1.5	1.5	-9.0	0.0	-9.0	3.5	0.5	0.5	-3.0	0.0	-3.0	-	-	-	-	-
Athyrium filix-femina	89.6	98.5	23.9	9.0	-74.6	-65.7	128.5	330.0	67.0	201.5	-263.0	-61.5	3	x	7	x	6
Chaerophyllum aromaticum	10.4	3.0	0.0	-7.5	-3.0	-10.4	3.5	1.0	0.0	-2.5	-1.0	-3.5	7	5	7	6	8
Chrysosplenium alternifolium	17.9	1.5	0.0	-16.4	-1.5	-17.9	6.0	0.5	0.0	-5.5	-0.5	-6.0	4	4	8	7	5
Corylus avellana	35.8	19.4	11.9	-16.4	-7.5	-23.9	12.0	6.5	9.0	-5.5	2.5	-3.0	6	5	x	x	5
Daphne mezereum	44.8	10.4	3.0	-34.3	-7.5	-41.8	15.0	3.5	1.0	-11.5	-2.5	-14.0	4	x	5	7	5
Galeopsis speciosa	7.5	22.4	0.0	14.9	-22.4	-7.5	2.5	7.5	0	5.0	-7.5	-2.5	7	x	5	x	8
Gentiana asclepiadea	11.9	1.5	4.5	-10.4	3.0	-7.5	6.5	0.5	4.0	-6.0	3.5	-2.5	7	x	6	7	2
Geranium phaeum	23.9	11.9	3.0	-11.9	-9.0	-20.9	8.0	4.0	6.0	-4.0	2.0	-2.0	6	x	5	6	5
Glechoma hirsuta	52.2	55.2	20.9	3.0	-34.3	-31.3	52.5	31.0	51.5	-21.5	20.5	-1.0	-	-	-	-	-
Lonicera xylosteum	23.9	6.0	0.0	-17.9	-6.0	-23.9	8.0	2.0	0.0	-6.0	-2.0	-8.0	5	6	5	7	6
Mercurialis perennis	74.6	71.6	53.7	-3.0	-17.9	-20.9	409.5	175.5	307.0	-234.0	131.5	-102.5	2	x	x	8	7
Oxalis acetosella	65.7	74.6	41.8	9.0	-32.8	-23.9	314.5	71.5	109.5	-243.0	38.0	-205.5	1	x	5	4	6
Phyteuma spicatum	10.4	4.5	0.0	-6.0	-4.5	-10.4	3.5	1.5	0.0	-2.0	-1.5	-3.5	x	x	5	6	5
Polygonatum multiflorum	55.2	44.8	13.4	-10.4	-31.3	-41.8	18.5	15.0	9.5	-3.5	-5.5	-9.0	2	x	5	6	5
Populus tremula	11.9	1.5	1.5	-10.4	0.0	-10.4	4.0	0.5	0.5	-3.5	0.0	-3.5	6	5	5	x	x
Primula elatior	9.0	6.0	0.0	-3.0	-6.0	-9.0	3.0	2.0	0.0	-1.0	-2.0	-3.0	6	x	6	7	7
Ribes uva-crispa	40.3	25.4	7.5	-14.9	-17.9	-32.8	13.5	8.5	10.0	-5.0	1.5	-3.5	4	5	x	x	6
Sambucus racemosa	11.9	14.9	3.0	3.0	-11.9	-9.0	4.0	5.0	3.5	1.0	-1.5	-0.5	6	4	5	5	8
Sanicula europaea	28.4	10.4	7.5	-17.9	-3.0	-20.9	9.5	6.0	7.5	-3.5	1.5	-2.0	4	5	5	8	6
Stellaria nemorum	19.4	40.3	0.0	20.9	-40.3	-19.4	9.0	13.5	0.0	4.5	-13.5	-9.0	4	x	7	5	7
Symphytum tuberosum	11.9	10.4	1.5	-1.5	-9.0	-10.4	4.0	20.5	3.0	16.5	-17.5	-1.0	5	8	5	6	7
Viburnum opulus	13.4	0.0	0.0	-13.4	0.0	-13.4	4.5	0.0	0.0	-4.5	0.0	-4.5	6	5	x	7	6

Table 4. Continuation.

	Frequency of occurences (%)			Changes in frequency of occurence (%)			Total abundance (sum of the mid-point percentage cover values)			Changes in abundance (%)			Ellenberg indicator values (EIVs)				
	1970s	2000s	2010s	First study period	Second study period	Total study period	1970s	2000s	2010s	First study period	Second study period	Total study period	L	T	F	R	N
Viola reichenbachiana	19.4	23.9	9.0	4.5	-14.9	-10.4	9.0	8.0	5.5	-1.0	-2.5	-3.5	4	x	5	7	6
Abies alba	71.6	70.1	50.7	-1.5	-19.4	-20.9	26.5	23.5	141	-3.0	117.0	114.0	3	5	x	x	x
Actaea spicata	61.2	41.8	17.9	-19.4	-23.9	-43.3	20.5	14	38	-6.5	24.0	17.5	3	5	5	6	7
Carex pilosa	53.7	47.8	40.3	-6.0	-7.5	-13.4	687.5	847.5	730.5	160.0	-117.0	43.0	4	6	5	5	5
Circaea lutetiana	46.3	56.7	38.8	10.4	-17.9	-7.5	18.0	33.5	113.5	15.5	80.0	95.5	4	5	6	7	7
Dentaria bulbifera	91.0	91.0	74.6	0.0	-16.4	-16.4	320	463	323	142.5	-140.0	2.5	3	5	5	7	6
Euphorbia amygdaloides	26.9	26.9	14.9	0.0	-11.9	-11.9	11.5	11.5	20.0	0.0	8.5	8.5	4	5	5	8	5
Fraxinus excelsior	38.8	61.2	10.4	22.4	-50.7	-28.4	15.5	93.5	28.0	78.0	-65.5	12.5	4	5	x	7	7
Milium effusum	46.3	47.8	35.8	1.5	-11.9	-10.4	15.5	21.0	54.0	5.5	33.0	38.5	4	x	5	5	5
Paris quadrifolia	44.8	56.7	25.4	11.9	-31.3	-19.4	15.0	19.0	26.0	4.0	7.0	11.0	3	x	6	7	7
Petasites albus	46.3	28.4	20.9	-17.9	-7.5	-25.4	106.5	43.5	158.0	-63.0	114.5	51.5	4	4	6	x	5
Prenanthes purpurea	9.0	9.0	1.5	0.0	-7.5	-7.5	3.0	3.0	3.0	0.0	0.0	0.0	4	4	5	5	5
Scrophularia nodosa	16.4	14.9	4.5	-1.5	-10.4	-11.9	5.5	5.0	6.5	-0.5	1.5	1.0	4	5	6	6	7
Symphytum cordatum	68.7	68.7	59.7	0.0	-9.0	-9.0	243.5	281.0	160.5	37.5	-120.5	-83.0	-	-	-	-	-
Ulmus glabra	23.9	35.8	10.4	11.9	-25.4	-13.4	22.5	12.0	13.5	-10.5	1.5	-9.0	4	5	6	7	7
Carex digitata	4.5	9.0	0.0	4.5	-9.0	-4.5	1.5	3.0	0.0	1.5	-3.0	-1.5	3	x	5	x	4
Cerasus avium	1.5	6.0	0.0	4.5	-6.0	-1.5	0.5	2.0	0.0	1.5	-2.0	-0.5	-	-	-	-	-
Circaea alpina	4.5	7.5	0.0	3.0	-7.5	-4.5	1.5	2.5	0.0	1.0	-2.5	-1.5	4	4	7	5	5
Dentaria glandulosa	61.2	46.3	61.2	-14.9	14.9	0.0	275.0	86.5	220.5	-188.5	134.0	-54.5	-	-	-	-	-
Euonymus europaea	6.0	13.4	0.0	7.5	-13.4	-6.0	2.0	4.5	0.0	2.5	-4.5	-2.0	6	5	5	8	5
Rubus idaeus	3.0	14.9	0.0	11.9	-14.9	-3.0	1.0	19.5	0.0	18.5	-19.5	-1.0	7	x	x	x	6
Mixed reaction																	
Fagus sylvatica	59.7	92.5	38.8	32.8	-53.7	-20.9	39.5	53.0	120.5	13.5	67.5	**81.0**	3	5	5	x	x
Galeobdolon luteum	92.5	95.5	83.6	3.0	-11.9	-9.0	258.5	480.0	714.5	221.5	234.5	**456.0**	-	-	-	-	-
Geranium robertianum	52.2	19.4	20.9	-32.8	1.5	-31.3	20.0	6.5	53.5	-13.5	47.0	**33.5**	5	x	x	x	7
Pulmonaria obscura	73.1	58.2	14.9	-14.9	-43.3	-58.2	49.5	19.5	54.0	-30.0	34.5	**4.5**	4	5	6	8	7

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Climate and Management Factors Underlying Changes in Beech Forest Herbaceous Layer Plant Communities in the Polish Eastern Carpathians

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Abstract: The herbaceous vegetation and forest stand characteristics in European beech forests growing in the Polish part of the Eastern Carpathians have changed over the last 40 years. This has been influenced by many factors, including land-use change, forest management and climate change. This study investigates changes in forest cover and structure and the associated changes in herbaceous layer plant communities and seeks to elucidate whether and how beech forest herbaceous layer communities have been affected by climate change. The study used information from archival and current land cover maps, semi-permanent sampling plots, forest management plans for the Forest Districts of Brzozów, Lesko and Ustrzyki Dolne and meteorological weather station data compiled for three study periods of herbaceous vegetation (1970s, 2000s, 2010s). In the study area, the regular shelterwood system was changed to an irregular shelterwood system that produces stands with a complex overstorey structure. The results revealed the important role of light availability in shaping the species composition of the herbaceous layer in semi-natural Carpathian beech forests, which was strongly related to the course of management activities. An overall decrease in the number of species during the 2010s is linked to the ageing of beech forests, increased intensity of management activities in ageing stands, competition from understorey vegetation and lower soil moisture that can be linked to climate change. Our study partially supports the existing findings that more manipulative forest management systems can play an important role in countering the current and expected effects of climate change on the forest ecosystem because of the low degree of spatial differentiation of the stand's structure (developmental stages). Therefore, foresters managing the structure of stands should strive to create a forest structure with high variability of developmental stages on a regional scale.

Keywords: long-term studies; forest stands; forest management plans; East Carpathians; forest management; global warming

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1. Introduction

Forests are highly complex terrestrial ecosystems that have important environmental, social and economic functions [1–4]. Forests shape climate, regulate the water cycle, prevent floods and protect soil from erosion. Forests provide wood and other non-timber forest products, such as mushrooms and herbs. They also provide conditions that support a large number of species, conserving genetic resources and protecting ecosystem services [5–8].

Forests, like other ecosystems, are shaped by direct and indirect human activities [9,10]. Direct activities include the modification of stand structure by forest management, the spread of invasive species, timber harvesting and the use of non-timber forest services and functions [1,11,12]. The effects of indirect human activities include climate change, land-use change, changes in forest cover over time, as well as nitrogen accumulation and air pollution [13–17].

It is likely that changes In the case of European beech forests in the Polish part of the Eastern Carpathians can be attributed primarily to altered land use (abandonment of agricultural land and its afforestation), changes in forest management systems and climate change. The sudden decrease in population density after World War II as a result of political displacement played a key role in the conversion of agricultural land to forest [18,19]. Before World War II, the population density in the Polish part of the Eastern Carpathians was 100 people per 100 ha of agricultural land [20]. In contrast, in post-war censuses, these areas contained less than 30% of the pre-war population [21]. This decrease in population density resulted in the abandonment of agricultural land, allowing forests to develop through natural succession or by afforestation [22–25]. As a result, forest cover has increased and forest fragmentation decreased, which should benefit the maintenance and spread of herbaceous forest species, especially species with slow dispersal rates, e.g., myrmecochores [26,27].

The change in land use is also linked with the abandonment of non-agricultural forest uses by the surrounding farming population. After World War II, practices such as firewood collection, raking forest floor litter and use of forests as grazing land for livestock gradually disappeared in the Polish region of the Eastern Carpathians [28,29]. The decrease in the intensity of incidental forest use by the surrounding population was primarily due to the aforementioned population displacement. In subsequent years, the intensification of livestock farming and the legal prohibition of such activities have contributed to increases in forest area [29,30]. One of the consequences of decreased non-agricultural uses of the forest has been increased organic matter accumulation on the forest floor, which should increase the amount of nutrients available to shallow-rooting herbaceous species [31–33].

Before World War II, Poland's forests were heavily exploited. Timber harvesting exceeded growth, and mainly targeted the oldest stands, which were felled on vast areas, often using clearcutting [34]. In the Polish part of the Eastern Carpathians, between 1950 and 1990, the regular shelterwood system (with a stand regeneration period of 10–20 years, resulting in single-storey stands with little age differentiation) began to be applied. Then, in the second half of the 1990s, the regular shelterwood system was replaced by the irregular shelterwood system [35,36]. In the irregular shelterwood system, felling and subsequent regeneration take place over a period of 30–50 years. In this management system, it is possible to use a variety of cut types adapted to the needs of the species for regeneration (edge cuts on groups and streaks, shelterwood and selected cuts, and even complete cuts on small areas). The cuts in a given forest sub-compartment usually take place every 3–6 years, resulting in stands with a complex overstorey structure and a large diversity of stand ages. Irregular shelterwood management is accompanied by long-term changes in the amount of light reaching the forest floor. The resulting gaps in the stand, which are widened during successive cuttings, are successively filled by understorey species. Thus, the competitive impact of understorey growth mainly by European beech (*Fagus sylvatica* L.) growing in dense clumps seems to have an important impact on herbaceous vegetation in beech forests. Beech appears to be a strong competitor for nutrients and water [37]. Forest management practices (size of harvested area, type of cut, length of regeneration period) have significant impacts on the diversity of its communities because they change short-term and long-term habitat conditions (mainly the amount of light reaching the forest floor and humidity) and create favourable conditions or limitations for seed dispersal. In the Polish part of the Eastern Carpathians, the proportion of tree stands over 100 years old is 38.5% (Forest Districts of Brzozów, Lesko and Ustrzyki Dolne). In this type of ageing beech stands, tree species diversity is lower, with beech being a strong competitor with other tree species, displacing them in later stages of forest development [38]. This affects the quality of forest litter, with changes in the amount of available nutrients and the acidification of topsoil [39,40].

The final factor affecting herbaceous layer plant communities addressed in this study is climate change. In recent decades, the impact of climate change on European beech forests has been considered primarily in the context of changes in forest stand structure. Droughts and low amounts of rainfall reduce the annual growth of trees. It was also found that diversified species composition may contribute to better stand stability during climate change [41–45]. In the Carpathians, between 1881 and 2009, the annual mean temperature has increased by about 1.6 °C [46]. Higher temperatures cause faster soil warming in the spring and this promotes the earlier onset of plant growth, increasing the proportion of thermophilic species in plant communities [47,48]. The decline in precipitation in recent years translates into lower topsoil moisture [49]. Lower water availability during the growing season can affect productivity and shift the species composition of forest ecosystems [50]. Zellweger et al. [48] indicated that the microclimate dependent on the tree and shrub cover has a greater influence on forest herbaceous vegetation than the macroclimate. Hence, managing stands so that the total tree cover and shrub layer do not decrease in the coming years is likely to mitigate some of the changes caused by rising temperatures, which may reduce the spread of thermophilic species.

The aim of this study was to follow (1) changes in the cover and structure of forest stands in the Polish Eastern Carpathians and (2) changes in beech forest herbaceous layer plant communities occurring against this background. Additionally, this study addresses question (3) of whether and to what extent herbaceous layer plant communities may be affected by climate change.

2. Materials and Methods

2.1. Study Area

The study area encompassed three Forest Districts—Brzozów, Lesko and Ustrzyki Dolne, in the Polish Eastern Carpathians (49°33′6.900″ N; 22°20′42.225″ E, Figure 1), with a total area of 1731.15 km^2. Most of this area is located in the mesoregion Sanocko-Turczańskie Mountains, Dynów Foothills and Bukowiec Foothills. The soils are dominated by brown soils formed from Carpathian flysch [51,52]. In the period 1966–2018, the average annual temperature was 7.7 °C, with an annual rainfall of 820.8 mm (data from the Lesko station, 420 m a.s.l. [53]). Beech forms the dominant forest type, with a phytosociological classification of *Dentario glandulosae Fagetum* Klika 1927 em. Mat. 1964. Beech forests in the Polish part of the Carpathians cover 25.3% of the total land area and the species is one of the most important in this region [54].

Over 90% of the stands within the area have protective functions, mainly reducing soil erosion and impoverishment and protecting surface and groundwater. This area is a part of the Natura 2000 network (“Ostoja Góry Słonne” PLH180013 and “Góry Słonne” PLB180003), including the Słonne Mountains Landscape Park and thirteen nature reserves.

2.2. Data Collection

Data from the three Forest Districts, Brzozów, Lesko and Ustrzyki Dolne, were used to assess stand structure and forest use. We chose these Forest Districts because they encompassed semi-permanent sampling plots intended for long-term observation of vegetation in the fertile mountain beech forests (Figure 1, [40,51]).

Changes in forest cover were evaluated using maps of spatial data of forest distribution in the Polish Carpathians in the 1860s, 1930s and 1970s, developed as part of the FORECOM project [24]. Forest cover in the 2000s and 2010s was determined on the basis of data from the CORINE Land Cover project [55], where satellite images were used to plot land use. Vector graphics denoting forests in each year were trimmed to the study area and forest area and forest cover in subsequent periods were calculated, with changes visualised using ArcMap 10.7 (ESRI, Redlands, CA, USA).

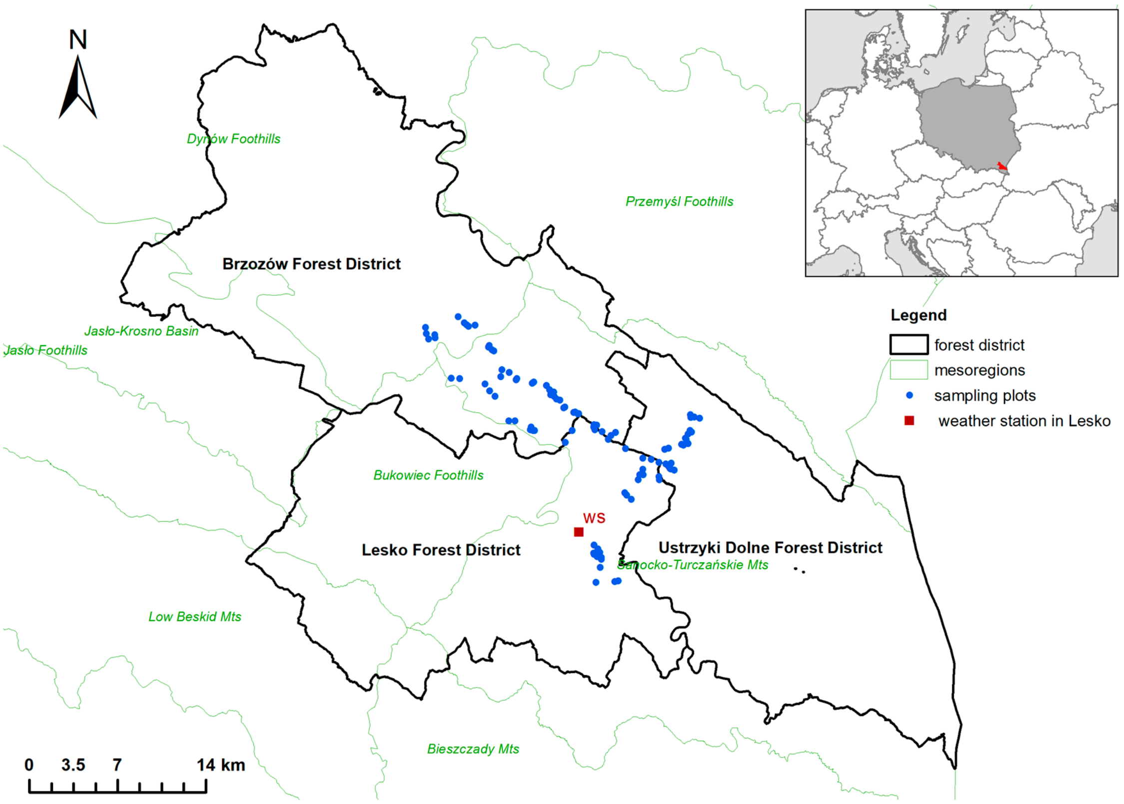

Figure 1. Location of the study site.

In order to analyse changes in age and species structure of forest stands, data of forest area by age class for dominant species was obtained from forest management plans for three time periods (adjusted to the herbaceous vegetation research periods) for each Forest District: Brzozów (1976, 2007, 2017), Lesko (1976, 2009, 2019) and Ustrzyki Dolne (1977, 2009, 2019). Age class was assigned based on the age of the dominant tree species in 20-year age-class categories (I—1–20 years; II—21–40 years; III—41–60 years; IV—61–80 years; V—81–100; VI—101–120; VII—more than 121 years). Stands in the regeneration phase and in the "for-regeneration" class, i.e., in which felling is about to be carried out, are designated "RP" (regeneration period).

To track changes in herbaceous layer plant communities and percentage cover by tree species, we used data from phytosociological relevés covering a period of 40 years made using the Braun–Blanquet method [56] in three research periods (in the years 1972–1973, 2005–2007 and 2017–2018). These datasets were collected from 67 semi-permanent sampling plots used for long-term observation of vegetation [40,51].

Because of the fine-grained differentiation of microclimatic conditions in forests on mountain areas, we placed great emphasis on the accuracy of the location of resurveyed plots. To do it, during the reestablishment of the sampling plots in the 2000s, we used the 1970s source materials ([51] and a 1:45,000 scale unpublished map that was drawn by Dzwonko during his study) and marked them by geographic coordinates. During every resampling period, we verified the location of sampling plots using descriptions (exposition inclination and altitude) given by Dzwonko [51]. To make the phytosociological data from three research periods comparable, the vegetation records during resampling were taken from plots with the same area and during the growing season, as in the 1970s. Moreover, we checked if the differentiation in localization of sampling plots could have an impact on results. We found that most of the sampling plots were located in a relatively narrow gradient of a.s.l. and inclination (500–650 m a.s.l. and 5–15 degrees) and quite evenly spaced in relation to the main exposures (NSEW, 12, 15, 10, 11). Therefore we did not address the issue of the impact of microhabitats on changes in the herbaceous layer when generalizing the materials of field observations.

To evaluate changes in climate, meteorological data from 1966 to 2018 provided by the Institute of Meteorology and Water Management—National Research Institute [53] from the Lesko station (420 m a.s.l.) were used. Average temperatures and precipitation were calculated for ten-year periods (1966–1975; 1999–2008; 2009–2018). The range of years coincides with the ten-year periods covered by forest management plans, during which phytosociological surveys were carried out on semi-permanent sampling plots. Climate data for the months of the growing season, i.e., April to August, were used to compare research periods, similar to Bosela et al. [43] and Thom et al. [57].

2.3. Analysis of Forest Vegetation

Changes in herbaceous layer plant communities in beech forests were analysed using data generated from phytosociological relevés from the 1970s, 2000s and 2010s. Total cover of the tree and shrub layer defined according to Ewald et al. [58] (Total_Cov), herbaceous cover (Herb_Cov), number of herbaceous species (Number_Herb) and number of seedlings (Number_Seedl) of woody species in the study plots were compared for each period of research. Ecological groups of species were identified and compared, specifically for (1) ancient forest plant species (Number_Ancient) (as described by Hermy et al. [59] and Dzwonko and Loster [60], these are forest plant species that are very slow to colonize a habitat and whose presence indicates long-term site stability) and (2) species characteristic of beech forests (S_beech_forest) as described in phytosociological nomenclature by Matuszkiewicz [61]. Additionally, for each phytosociological relevé, the number of species representing fast- and slow-dispersing species groups was calculated. Fast-dispersing species include anemochores (ANE)—dispersal by wind; endozoochores (END)—dispersal by animals via digestion; epizoochores (EPI)—dispersal by adhesion on animals. Slow-dispersing species include myrmecochores (MYR)—dispersal by ants; hydrochores (HYD)—dispersal by water; baro- and autochores (BAR and AUT)—passive and active dispersal by plants [59,60]. In addition, for each phytosociological relevé from the three study periods, the Ellenberg indicator values (EIVs, [62]) were calculated based on species presence/absence in phytosociological relevés. Among the EIVs, the Ellenberg indicators for light (L), temperature (T), soil moisture (F), soil reaction (R), and soil nitrogen (N) were selected. These indicators enabled changes in habitat conditions to be determined indirectly [63]. To calculate the Total_cov, Braun–Blanquet cover-abundance values of each species in the tree and shrub layer were converted to average per cent cover values.

For identifying species indicative of a given research period, we used indicator species analysis [64]. For this purpose, we used herbaceous plants with a total attendance of at least 5%. The statistical significances of the species indicator values (IndVal) were estimated by 9999 random permutations of plots across sampling periods. We expected that the ecological preferences of the obtained groups of indicator species would contribute to the identification of the drivers of changes in forest vegetation.

Differences between scores obtained for the 1970s, 2000s and 2010s were tested using repeated measures tests. Depending on data distribution, either the ANOVA or the Friedman test was applied, followed by a posteriori Tukey's or Wilcoxon's test with Bonferroni correction, respectively. Statistical analyses were calculated using PAST software version 4.03 (Øyvind Hammer, Natural History Museum, University of Oslo, Oslo, Norway) [65].

The analyses did not take into account early spring herbaceous species, which were excluded to avoid errors resulting from shifts in the onset of the spring season. To avoid errors resulting from incorrect identification of similar species, *Senecio nemorensis* and *S. fuchsii*, as well as similar ferns species from the genus *Dryopteris*, were combined into one group.

3. Results

3.1. Changes in Forest Cover

Forest cover within the study boundaries almost doubled from 1860 to 2018 (from 43,679 ha to 82,408 ha, Figure 2). The greatest increase in forest cover occurred between the 1930s and 1970s. During this period, forest cover increased from 26.1% to 42.8%, which was mainly due to depopulation processes. In subsequent years, forest cover continued to grow, but at a much slower rate, reaching 47.6% in the 2010s.

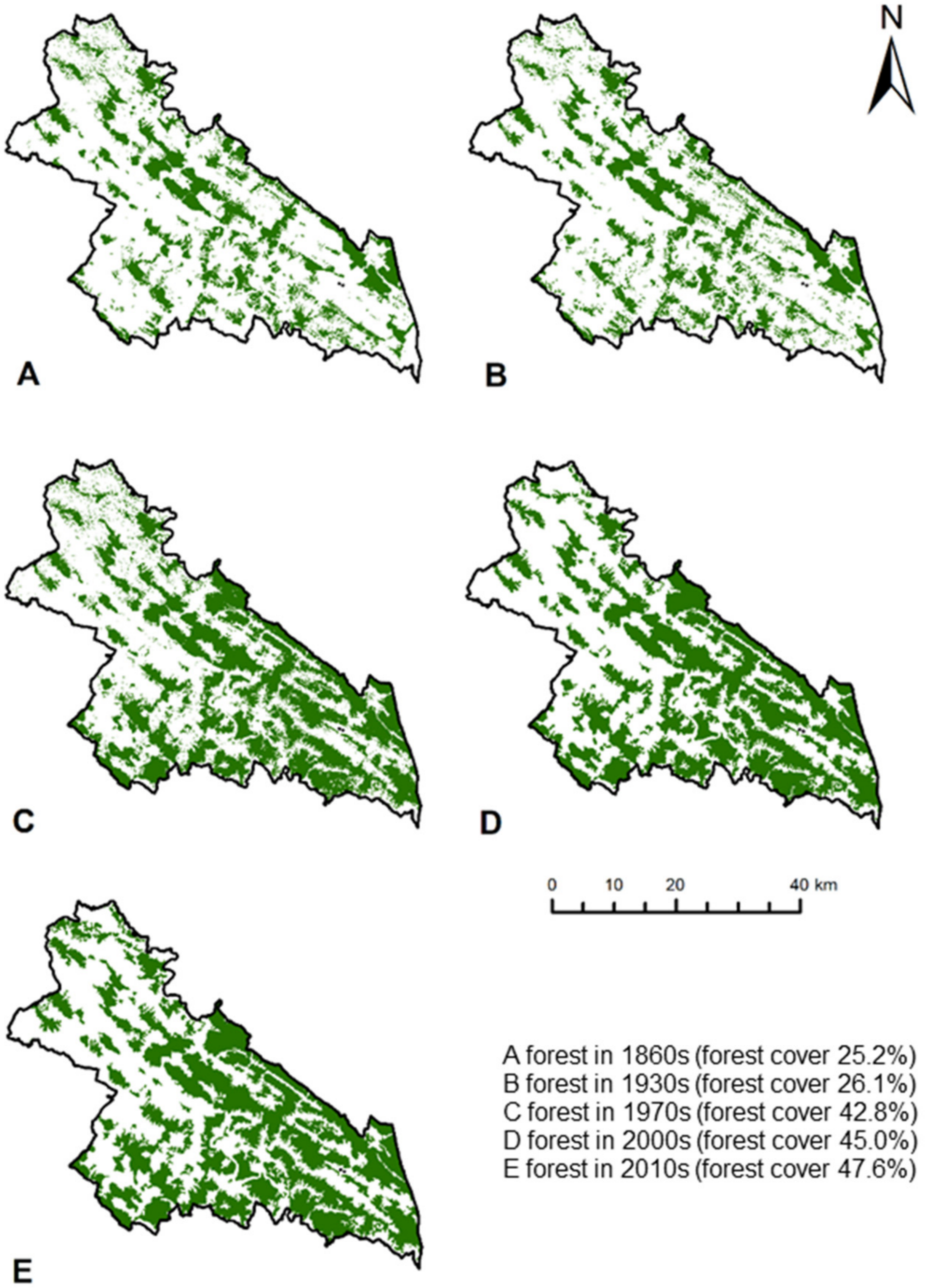

Figure 2. Changes in forest cover over time.

3.2. Changes in Stand Structure and Forest Management

The age structure and dominant species of forest stands changed significantly from the 1970s to 2010s (Figure 3). In the 1970s, stands in the 21–40-year age class dominated (32.6%). In the 2000s, most stands fell within the 41–60-year class, followed by regenerating

(RP) stands (27.3%). In the 2000s and 2010s, RP stands accounted for the largest area (27.3% and 28.6%, respectively).

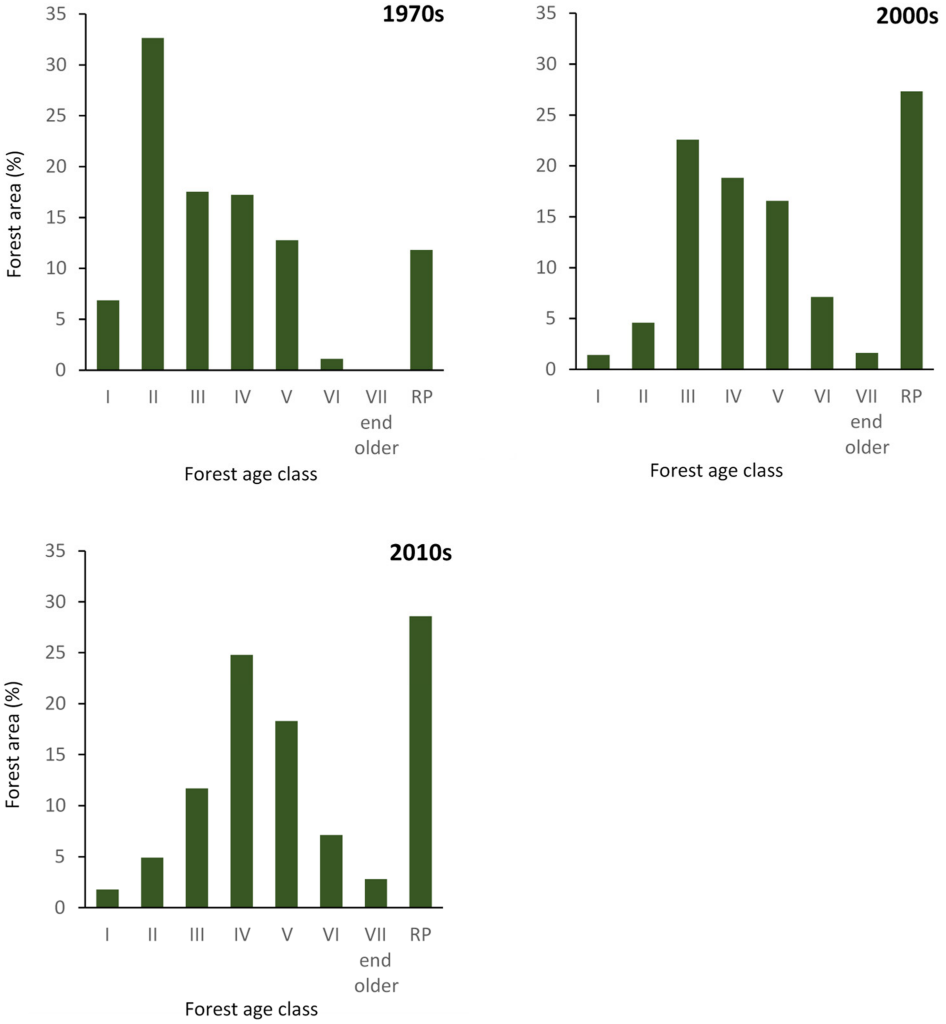

Figure 3. Proportion of forest area by age class (RP—stands in the regeneration period) in the 1970s, 2000s and 2010s.

Between the 1970s and 1990s forests in Brzozów, Lesko and Ustrzyki Dolne Forest Districts were regenerated using the regular shelterwood system. This created even-aged, one-storied stands, which can be seen in Figure 3 for the 1970s, where the differentiation of age classes III–V was small. At the end of the 1990s, management was changed to the group shelterwood and irregular shelterwood systems. In subsequent years, management was primarily by the irregular shelterwood system, which produces irregular stand structures even on small spatial scales. A clear age differentiation was evident in the 2010s, with a large share of stands still classified as regenerating. The predominance of regenerating stands will continue in the coming decades because the irregular shelterwood system is characterized by a long regeneration period (lasting from 30 to 50 years).

3.3. Changes in Beech Forest Communities

Based on data from forest management plans, between the 1970s and 2010s the share of stands with beech as the dominant species increased from 27.6% to 34.1% (Table 1). These results are confirmed by data from study plots, where the percentage cover of beech between the 1970s and 2010s increased on average from 47.4% to 54.9% (Table 2). Moreover, between the 2000s and 2010s, the average percentage cover of admixture tree species changed, with fir (*Abies alba*) increasing from 10.4% to 14.1% while sycamore (*Acer pseudoplatanus*) decreased from 8.6% to 7.3% and ash (*Fraxinus excelsior*) from 2.7% to 0.1% (Table 2).

Table 1. Percentages of dominant tree species in forest stands during the 1970s, 2000s and 2010s. Data are from Forest Management Plans. The table includes species whose percentage share was greater than 0.1.

Species	Year		
	1970s	2000s	2010s
	%		
Pinus sylvestris L.	21.7	22.0	20.9
Larix decidua Mill.	1.0	2.5	2.6
Picea abies (L.) H. Karst.	2.4	2.9	2.7
Abies alba Mill.	28.2	27.0	30.9
Fagus sylvatica L.	27.6	31.4	34.1
Quercus robur L.	1.4	1.6	1.1
Acer pseudoplatanus L.	1.0	4.1	3.0
Fraxinus excelsior L.	0.1	0.8	0.3
Carpinus betulus L.	3.2	2.0	1.6
Betula pendula Roth	4.3	1.7	0.8
Alnus glutinosa (L.) Gaertn.	0.2	0.2	0.2
Alnus incana (L.) Moench	8.5	3.6	1.6
Populus tremula L.	0.2	0.1	0.1
Salix sp.	0.0	0.2	0.0

Table 2. Mean percentage of canopy tree species in semi-permanent sampling plots.

Species	Year		
	1970s	2000s	2010s
	%		
Fagus sylvatica	47.43	54.04	54.85
Abies alba	10.54	10.43	14.08
Acer pseudoplatanus	7.11	8.58	7.33
Fraxinus excelsior	1.49	2.74	0.06
Carpinus betulus	0.19	0.28	0.56
Tilia cordata Mill.	0.01	0.00	0.22
Acer platanoides L.	0.00	0.28	0.72
Pinus sylvestris	0.03	0.00	0.00
Larix decidua	0.01	0.00	0.00
Populus tremula	0.02	0.00	0.00
Quercus robur	0.02	0.01	0.00
Ulmus glabra Huds.	0.28	0.65	0.00

In the 2010s there was less herbaceous layer cover (Table 3) and a lower mean number of herbaceous plant species per study plot than in previous study periods. The average number of ancient forest and beech forest characteristic species also decreased significantly compared to the 1970s and 2000s. In addition, the average number of species with fast and slow seed dispersal in the 2010s was lower than in the 1970s. However, species with slow-dispersing seeds showed significant differences between all study periods, with the highest number of slow dispersal species found in the 2000s.

Table 3. Changes in variables obtained based on research at semi-permanent sampling plots over time. Values with different superscript letters differed significantly based on Tukey's or Wilcoxon's posteriori tests at the p level, at least $p \leq 0.05$. F and Chi^2—ANOVA and Friedman test score, respectively.

Variables	**Unit**	**Test Score**	**Mean (±SE) Values**		
		F, $^{\times}$Chi^2	**1970s**	**2000s**	**2010s**
Total_Cov	%	$^{\times}$0.96	88.0 (±0.97) ^{ns}	86.0 (±0.96) ^{ns}	85.5 (±1.74) ^{ns}
Herb_Cov	%	3.8 *	81.9 (±1.86) ^{a}	80.7 (±1.90) ^{a}	75.2 (±2.24) ^{b}
Number_Herb	-	36.9 ***	24.5 (±0.84) ^{a}	26.9 (±0.95) ^{a}	18.4 (±0.71) ^{b}
Number_Seedl	-	$^{\times}$59.0 ***	5.5 (±0.27) ^{a}	6.0 (±0.23) ^{a}	3.0 (±0.17) ^{b}
Number_Ancient	-	$^{\times}$52.1 ***	18.7 (±0.69) ^{a}	20.0 (±0.80) ^{a}	12.3 (±0.49) ^{b}
S_beech_forest	-	7.0 ***	3.9 (0.2) ^{a}	3.7 (0.2) ^{a}	3.1 (0.2) ^{b}
Fast species (ANE, END, EPI)	-	$^{\times}$44.5 ***	7.9 (±0.37) ^{a}	7.7 (±0.36) ^{a}	4.4 (±0.22) ^{b}
Slow species (MYR, HYD, BAR, AUT)	-	$^{\times}$46.6 ***	4.7 (±0.24) ^{a}	6.0 (±0.30) ^{b}	3.0 (±0.22) ^{c}
EIVs L	-	3.4 *	3.8 (±0.04) ^{a}	3.8 (±0.03) ^{a}	4.0 (±0.05) ^{b}
EIVs T	-	2.3	5.0 (±0.01) ^{ns}	5.0 (±0.02) ^{ns}	5.0 (±0.02) ^{ns}
EIVs F	-	4.1 *	5.6 (±0.02) ^{ab}	5.6 (±0.02) ^{a}	5.5 (±0.03) ^{b}
EIVs R	-	$^{\times}$10.2 **	6.5 (±0.04) ^{a}	6.3 (±0.06) ^{b}	6.4 (±0.07) ^{b}
EIVs N	-	$^{\times}$3.4	6.2 (±0.04) ^{ns}	6.2 (±0.06) ^{ns}	6.2 (±0.06) ^{ns}

* $p \leq 0.05$.; ** $p \leq 0.01$.; *** $p \leq 0.001$.

Analysis of habitat conditions based on Ellenberg indicator values showed that in the 2010s more light reached the forest floor and there was less soil moisture than in the 1970s and 2000s. In addition, in the 2000s and 2010s, the soil reaction was lower than in the 1970s (Table 3).

The indicator species analysis showed a large difference between the diagnostic species not only in terms of species composition (Figure 4) but also habitat requirements. In the 1970s, the diagnostic species were characterized by low light requirements (e.g., *Mercurialis perennis*, *Oxalis acetosella*, *Polygonatum multiflorum*) and moderate nitrogen demand (e.g., *Chrysosplenium alternifolium*, *Geranium phaeum*, *Petasites albus*, *Phyteuma spicatum*). In the 2000s, the diagnostic species had slightly higher light requirements and high nitrogen demand (e.g., *Anthriscus nitida*, *Stellaria nemorum*, *Veronica montana*). Their composition included species related to gaps formed in the stand during partial cutting of trees, such as *Galeopsis speciosa* and *Rubus idaeus*. In the 2010s, species of clearings with high demand for light and nitrogen dominated among diagnostic species (e.g., *Rubus hirtus*, *Rumex obtusifolius*, *Senecio fuschii* and *S. nemorensis*).

3.4. Climatic Conditions

The average temperature during the growing season (April to August), gradually increased over the three study periods: in the 1970s it was 13.7 °C, in the 2000s 14.6 °C and in the 2010s 15.1 °C (Figure 5). The average temperature increase between the 1970s and 2010s was 1.4 °C. Average precipitation during the growing season was significantly lower (463.8 mm) in the 2010s than in the 1970s (516.3 mm) or 2000s (513.7 mm) (Figure 6).

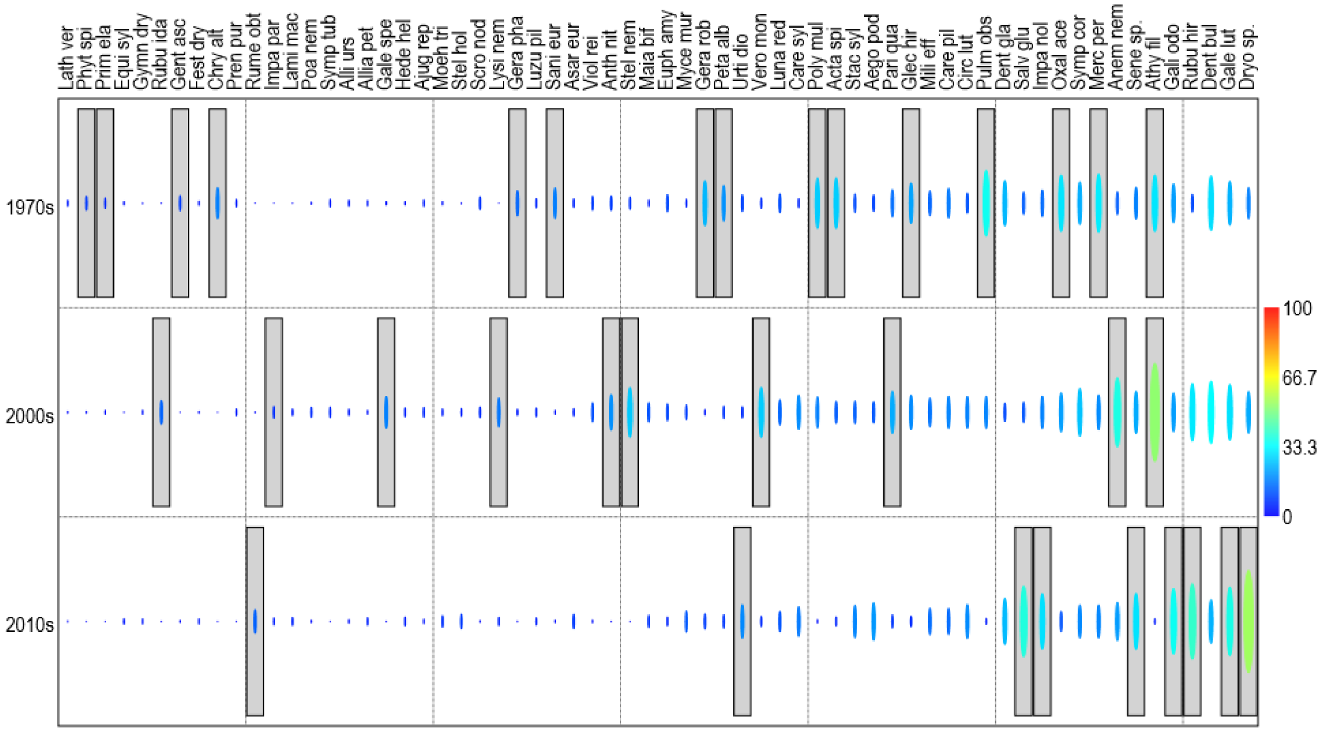

Figure 4. Results of indicator species analysis. Values of indicator value of species (IndVal%) for study periods are presented. The statistical significances ($p < 0.05$) of the indicator values have been boxed.

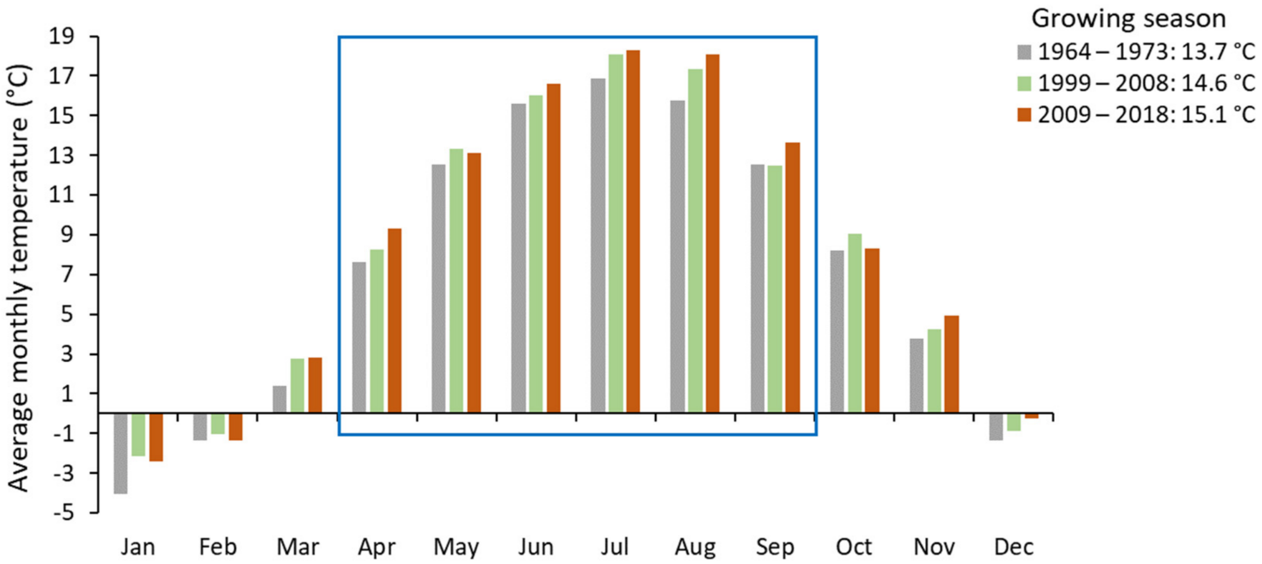

Figure 5. Average monthly temperature in the periods 1966–1975, 1999–2008 and 2009–2018 based on climate data from the Lesko weather station (420 m a.s.l.). The blue frame encloses months falling within the growing season.

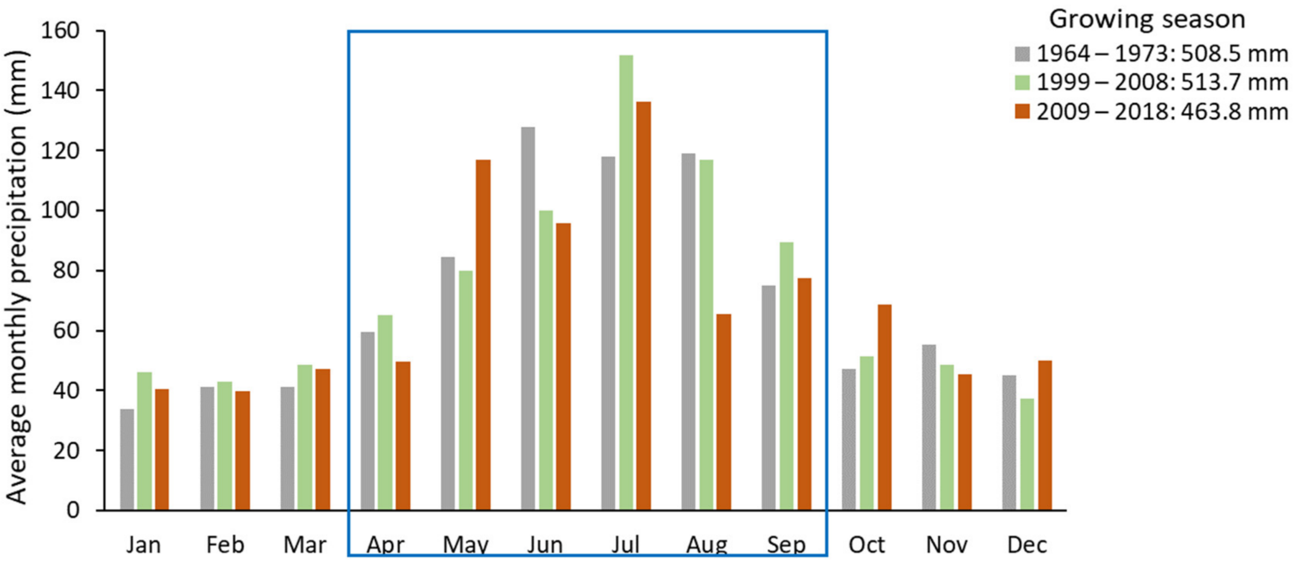

Figure 6. Average monthly precipitation in the periods 1966–1975, 1999–2008 and 2009–2018 based on climate data from the Lesko weather station (420 m a.s.l.). The blue frame encloses months falling within the growing season.

4. Discussion

4.1. Impact of Changes in Forest Area

Forest cover in the Brzozów, Lesko and Ustrzyki Dolne Forest Districts increased from 25.2% to 47.6% from the 1860s to 2010s, which is much higher than the average forest cover of 29.6% in Poland overall [66]. Increased forest cover has been generally observed since the 19th century in all European mountain ranges due to the abandonment of agricultural land as a result of progressive socio-economic changes (e.g., unprofitability of agricultural production in mountain areas, population migration to towns and employment opportunities outside the agricultural sector). Slow regeneration of forest vegetation has begun on abandoned agricultural land or has been accelerated by afforestation programs [23,67,68].

Changes in forest cover in the study area largely correspond to those observed overall in the Polish Carpathians, where forest cover increased from 27% to 47% from the mid-19th century to the 2010s [69,70]. This has resulted in the establishment of extensive forest complexes contributing to reduced forest fragmentation, especially in the southern and south-eastern parts of the Polish Carpathians [25]. New forest areas have been created in places where previously a different type of land use was exercised (e.g., fields, meadows, midfield afforestation). These areas were afforested with Scots pine (*Pinus sylvestris*), and in areas left to natural succession, the main forest tree species was grey alder (*Alnus incana*) [23,28]. Our study suggests that increased forest area and progressive reconstruction of species composition over time in stands on former farmland, followed by the restoration of forest habitats, had a positive effect on the species composition of herbaceous layer plant communities. Changes in herbaceous layer plant communities over time showed a greater number of slow-dispersing and ancient forest species in the 2000s than in the 1970s. The optimum conditions for these species in the 2000s are related to the dominant, optimum stage of stand development. In the 2010s, despite an increase in forest cover, there was a decrease in the number of beech and slow-dispersing species, which is probably related to the increased intensity of management in ageing stands [71].

4.2. Impact of Changes in Stand Structure and Forest Management

Stand spatial structure consists of the vertical and horizontal organisation of the trees. Stand structure affects herbaceous plant species composition and influences habitat conditions and microclimate [31,32,72]. In commercial forests, stand structure is shaped by the silvicultural system [36]. A change in management to one that more closely mimics natural forest regeneration processes results in a significant modification of spatial structure [73,74]. In the Polish part of the Eastern Carpathians, at the end of the 1990s, the regular shelterwood system that created single-storey and single-aged stands was replaced by the irregular shelterwood system, producing more diverse stand ages and overstorey structures [35]. In the 2000s and 2010s, compared to the 1970s, there was a significant increase in the proportion of stands of age class VI and those designated in the regeneration period (RP) and a decrease in younger stands of age classes II and III. Mean stand age changed from the 1970s to the 2010s from 85.3 to 113.0 years [71]. In timber production forests, older stand ages are accompanied by increased disturbance as a result of natural changes in forest development and intensified silvicultural activities related to felling and stand regeneration. As a result of natural forest ageing, tree species diversity decreases. In stands within the study area, decreased occurrence of valuable admixture species, i.e., sycamore and ash, may contribute to nutrient depletion and acidification of forest soils [39,75]. The results presented in this paper provide evidence of this outcome, since while there was no decrease in nutrient content (EIVs N), there was an increase in soil acidity (EIVs R) between the 1970s and 2010s.

Tree crown cover decreased over time in beech stands, from 87.3% in the 1970s to 84.0% in the 2000s and 77.6% in the 2010s. However, the resulting overstorey gaps were filled relatively quickly by understorey species, with cover reaching 27.2% in the 2010s [71]. As a result, there was only a slight, non-significant decrease in total tree and undergrowth layer cover (Total_Cov) between the three study periods. Although a reasonably constant level of total tree and shrub layer cover could be expected to translate into unaltered light and moisture conditions, there were changes in the light and moisture conditions on the forest floor, with increased available light (EIVs L) and decreased soil moisture (EIVs F) in the 2010s.

Valuable indicators of drivers of changes in forest vegetation turned out to be diagnostic species. They clearly showed the strong relationship between the herbaceous plant communities and the habitat conditions changing with the development of the forest stand. As the age of the stand increased (development of the stand), the amount of light reaching the forest floor increased as a result of self-thinning or management activities. The increasing amount of light contributed to a faster release of nutrients from the accumulating dead organic debris on the forest floor [76]. Hence, the herbaceous vegetation of the 2000s was characterized by far more occurrence of mesotrophic species of deciduous forests than in the 1970s. The intensification of treatments related to the renewal of mature stands in the 2010s significantly increased thinning of tree crowns and the inflow of light to the forest floor. This was well reflected in the development of species of clearings with high demand for light and nitrogen. The result of the indicator species analysis revealed the important role of light availability in shaping the species composition of the herbaceous layer in the Carpathian beech forests. Depauw et al. [77] came to similar conclusions when analysing temperate forests across Europe. In the studied Carpathian beech forests, despite their semi-natural character, the availability of light is strongly related to the course of management activities. It seems, therefore, that changes in herbaceous layer communities largely depend on forest management.

In commercial forests, herbaceous layer species composition is influenced by activities such as vehicle traffic and soil disturbance during tree felling and extraction [78]. Thus, in beech forests evaluated for this study, in the 2010s, the intensity of forest management associated with tree felling and increased stand regeneration processes may have translated into an overall decrease in the number of herbaceous plant species.

4.3. Impact of Climate Change

Forests have a particularly strong influence on the microclimate at all times of the year, with the growing season being the key period. Stand structure that influences forest microclimate can partially compensate for the negative effects of heat and drought and slow down thermophilization (i.e., increasing relative abundances of warm-adapted or warm-tolerant species combined with the disappearance of cold-adapted species) of plant communities [48,57]. In spite of the moderating influences of tree canopies on microclimates, climate change directly or indirectly affects forest plants and their communities. This impact is increased when crown thinning alters the local microclimate, increasing temperature and decreasing moisture at the forest floor [48,57]. Bosela et al. [43] found that in diverse forest ecosystems (multi-species stands with complex spatial structure), trees can better withstand the higher temperatures associated with a warming climate. Therefore, the decrease in the tree crown cover [71] and the simplification of stand species structure observed in investigated beech forests may, with time, increase the negative impacts of warming on the functioning of herb layer communities.

Over the last 40+ years, the average growing season temperature has increased and the average precipitation has decreased. In the 2000s, when the majority of stands were at the optimum forest development stage [79] and the intensity of management activities was moderate, the impact of climate change may have been buffered by the dense canopy layer. In the 2010s, these stands reached commercial ages and the intensity of felling increased, resulting in lower tree layer cover and much higher shrub layer cover [71]. The temperature in forest stands might be expected to change with increased felling, however, a comparison of EIVs T indices between the study periods suggests that the forest floor temperature did not greatly change. This can be attributed to the buffering role of the developing shrub layer. The decrease in growing season precipitation during the 2010s is another important result of this study, which in addition to changes in stand structure, was responsible for decreased soil moisture (EIVs F) during the 2010s. Lower soil moisture in the 2010s clearly contributed to altered herbaceous species composition in beech forests by eliminating plants requiring soils with high moisture [71].

Our study supports the conclusion that more manipulative forest management systems can play an important role in countering the current and expected effects of climate change on the forest ecosystem [80]. The diverse vertical structure of the forest can lower the temperature inside the forest and reduce the humidity [81]. Therefore, implemented in the 1990s, the irregular shelterwood system allows for greater flexibility in responding to climate change by growing multi-storey stands of unequal age, which consist of trees of various sizes. In an irregular shelterwood system, the timing of cutting and the selection of harvested trees can be much better adapted to the changing climate than in a regular shelterwood system. For example, in an irregular shelterwood system, a longer renewal period allows the canopy of trees to be kept much more compact during the replacement of generations than when removing mature trees with a regular shelterwood system. However, in the period of final felling of mature stands, even more manipulative management systems may not be sufficient to counter climate change. In the study area, in the 2010s, most of the stands reached the final stage of development associated with intensive tree felling and renewal processes [79]. In this case, the small, spatial differentiation of the stands in terms of structure (developmental stages) seems to be responsible for the decline in the species richness of the herbaceous layer, including species of moisture habitats. Hence, we suggest that, while managing the structure of stands, foresters should strive to create a forest structure with high variability of developmental stages on a regional scale.

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References

1. Führer, E. Forest functions, ecosystem stability and management. *For. Ecol. Manag.* **2000**, *132*, 29–38. [CrossRef]
2. Święcicki, Z. (Ed.) *Instrukcja Urządzania Lasu. Cz. 1. Instrukcja Sporządzania Planu Urządzenia Lasu dla Nadleśnictwa*; CILP: Warsaw, Poland, 2012. (In Polish)
3. Vedeld, P.; Angelsen, A.; Bojö, J.; Sjaastad, E. Forest environmental incomes and the rural poor. *For. Policy Econ.* **2007**, *9*, 869–879. [CrossRef]
4. Varma, V.K.; Ferguson, I.S.; Wild, I. Decision support system for the sustainable forest management. *For. Ecol. Manag.* **2000**, *128*, 49–55. [CrossRef]
5. *European Forest Ecosystems–State and trends EEA Report*; European Environment Agency: Copenhagen, Denmark, 2016; p. 5.
6. Aggestam, F.; Konczal, A.; Sotirov, M.; Wallin, I.; Paillet, Y.; Spinelli, R.; Lindner, M.; Derks, J.; Hanewinkel, M.; Winkel, G. Can nature conservation and wood production be reconciled in managed forests? A review of driving factors for integrated forest management in Europe. *J. Environ. Manage.* **2000**, *268*, 110670. [CrossRef]
7. Blicharska, M.; Angelstam, P.; Giessen, L.; Hilszczański, J.; Hermanowicz, E.; Holeksa, J.; Jacobsen, J.B.; Jaroszewicz, B.; Konczal, A.; Konieczny, A.; et al. Between biodiversity conservation and sustainable forest management—A multidisciplinary assessment of the emblematic Białowieża Forest case. *Biol. Conserv.* **2020**, *248*, 108614. [CrossRef]
8. Maier, C.; Winkel, G. Implementing nature conservation through integrated forest management: A street-level bureaucracy perspective on the German public forest sector. *For. Policy Econ.* **2017**, *82*, 14–29. [CrossRef]
9. Vitousek, P.M.; Mooney, H.A.; Lubchenco, J.; Melillo, J.M. Human Domination of Earth's Ecosystems. *Science* **1997**, *277*, 494–499. [CrossRef]
10. Bengtsson, J.; Nilsson, S.G.; Menozzi, P. Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manag.* **2000**, *132*, 39–50. [CrossRef]
11. Kindstrand, C.; Norman, J.; Boman, M.; Mattsson, L. Attitudes towards various forest functions: A comparison between private forest owners and forest officers. *Scand. J. For. Res.* **2008**, *23*, 133–136. [CrossRef]
12. Kindler, E. A comparison of the concepts: Ecosystem services and forest functions to improve interdisciplinary exchange. *For. Policy Econ.* **2016**, *67*, 52–59. [CrossRef]
13. Stephen, R.; Shifley, R.; Moser, K.; Nowak, D.J.; Miles, P.D.; Butler, B.J.; Aguilar, F.X.; DeSantis, R.D.; Greenfield, E.J. Five anthropogenic factors that will radically alter forest conditions and management need in the Northern United States. *For. Sci.* **2014**, *60*, 914–925. [CrossRef]
14. Ortiz, J.C.; Espinosa, C.I.; Dahik, C.Q.; Mendoza, Z.A.; Ortiz, E.C.; Gusmán, E.; Weber, M.; Hildebrandt, P. Influence of Anthropogenical Factors on the Diversity and Structure of a Dry Forest in the Central Part of the Tumbesian Region (Ecuador-Perú). *Forests* **2019**, *10*, 31. [CrossRef]
15. Gautam, K.H.; Devoe, N.N. Ecological and anthropogenic niches of sal (*Shorea robusta* Gaertn. f.) forest and prospects for multiple-product forest management—A review. *Forestry* **2006**, *79*, 81–101. [CrossRef]
16. Puettmann, K.J.; Wilson, S.M.; Baker, S.C.; Donoso, P.J.; Drössler, L.; Amente, G.; Harvey, B.D.; Knoke, T.; Lu, Y.; Nocentini, S.; et al. Silvicultural alternatives to conventional even-aged forest management—What limits global adoption? *For. Ecosyst.* **2015**, *2*, 8. [CrossRef]
17. Tylianakis, J.M.; Didham, R.K.; Bascompte, J.; Wardle, D.A. Global change and species interactions in terrestrial ecosystems. *Ecol. Lett.* **2008**, *11*, 1351–1363. [CrossRef]
18. Kuemmeerle, T.; Hostert, P.; Radeloff, V.C.; Perzanowski, K.; Kruhlov, I. Post-socialist forest disturbance in the Carpathian Border region of poland, Slovakia, and Ukraine. *Ecol. Appl.* **2007**, *17*, 1279–1295. [CrossRef]
19. Kuemmeerle, T.; Hostert, P.; Radeloff, V.C.; Linden, S.; Perzanowski, K.; Kruhlov, I. Cross-border Comparison of Post-socialist Farmland Abandonment in the Carpathians. *Ecosystems* **2008**, *11*, 614–628. [CrossRef]
20. Kubijowicz, W. *Życie Pasterskie w Beskidach Wschodnich*; Prace Instytutu Geografii UJ: Kraków, Poland, 1926. (In Polish)
21. Skała, M.; Wolski, J. Krajobraz (nie)pamięci–teraźniejszość nadpisująca przeszłość. Osadnictwo i ludowość. In *Bojkowszczyzna Zachodnia-Wczoraj, Dziś i Jutro, Tom 2*; Instytut Geografii i Przestrzennego Zagospodarowania in Stanisława Leszczyckiego Monografie: Warsaw, Poland, 2016; Volume 37, pp. 347–377. (In Polish)
22. Durak, T.; Żywiec, M.; Kapusta, P.; Holeksa, J. Impact of land use and climate changes on expansion of woody species on subalpine meadows in the Eastern Carpathians. *For. Ecol. Manag.* **2015**, *339*, 127–135. [CrossRef]
23. Kozak, J. Forest Cover Change in the Western Carpathians in the Past 180 Years. A Case Study in the Orawa Region in Poland. *Mt. Res. Dev.* **2003**, *23*, 369–375. [CrossRef]
24. Kozak, J.; Kaim, D. *Forecom*; Instytut Geografii i Gospodarki Przestrzennej UJ: Krakow, Poland, 2016. (In Polish)

25. Kozak, J.; Ziółkowska, E.; Vogt, P.; Dobosz, M.; Kaim, D.; Kolecka, N.; Ostafin, K. Forest-Cover Increase Does Not Trigger Forest-Fragmenntation Decrease: Case Study from the Polish Carpathians. *Sustainability* **2018**, *10*, 1472. [CrossRef]
26. Matlack, G.R.; Monde, J. Consequences of low mobility in spatially and temporally heterogeneous ecosystems. *J. Ecol.* **2004**, *92*, 1025–1035. [CrossRef]
27. Matlack, G.R. Slow plants in a fast forest: Local dispersal as a predictor of species frequencies in a dynamic landscape. *J. Ecol.* **2005**, *93*, 50–59. [CrossRef]
28. Marszałek, E. The forest management in the Carpathian part of Regional Directorate of the State Forest in Krosno and its influence on the protection of nature. *Rocz. Bieszcz.* **2011**, *19*, 59–75. (In Polish)
29. Varga, A.; Molnár, Z.; Biró, M.; Demeter, L.; Gellény, K.; Miókovics, E.; Molnár, Á.; Molnár, K.; Ujházy, N.; Ulicsni, V.; et al. Changing year-round habitat use of extensively grazing cattle, sheep and pigs in East-Central Europe between 1940 and 2014: Consequences for conservation and policy. *Agric. Ecosyst. Environ.* **2016**, *234*, 142–153. [CrossRef]
30. Ustawa z dnia 28 Września 1991 r. o Lasach. Dz. U. 1991 Nr 101 poz. 444 (t.j. Dz. U. z 2020 r. poz. 1463). Available online: https://isap.sejm.gov.pl/isap.nsf/DocDetails.xsp?id=WDU19911010444 (accessed on 16 March 2021). (In Polish)
31. Helmy, N.; Essl, F.; Mirtl, M.; Dirnoböck, T. Multiple environmental changes drive forest floor cegetation in a temperate mountain forest. *Ecol. Evol.* **2017**, *7*, 2155–2168. [CrossRef] [PubMed]
32. Jacob, M.; Weland, N.; Platner, C.; Schaefer, M.; Leuschner, C.; Thomas, F.M. Nutrient release from decomposing leaf litter of temperate deciduous forest trees along a gradient of increasing tree species diversity. *Soil Biol. Biochem.* **2009**, *41*, 2122. [CrossRef]
33. Verheyn, K.; Baeten, L.; De Frenne, P.; Bernhardt-Römermann, M.; Brunet, J.; Cornelis, J.; Decocq, G.; Dierschke, H.; Eriksson, O.; Hédl, R.; et al. Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *J. Ecol.* **2012**, *100*, 352–365. [CrossRef]
34. Majchrowska, A. The History of State Forest and Forestry in Poland. *Manag. North. Eur. For.* **2018**, *12*, 318–358. [CrossRef]
35. Jaworski, A.; Kołodziej, Z. Beech (*Fagus sulvatica* L.) forest of a selection structure in the Bieszczady Mountains (Southeastern Poland). *J. For. Sci.* **2004**, *50*, 301–312. [CrossRef]
36. Jaworski, A. *Hodowla Lasu. Tom, I. Sposoby Zagospodarowania, Odnawianie Lasu, Przebudowa i Przemiana Drzewostanów*; Powszechne Wydawnictwo Rolnicze i Leśne: Warsaw, Poland, 2018. (In Polish)
37. Ellenberg, H.; Leuscher, C. *Vegetation Mitteleuropas mit den Alpen in Ökologischer, Dynamischer und Historischer Sicht*; Ulmer: Stuttgart, Germany, 2010. (In German)
38. Mölder, A.; Streit, M.; Schmidt, W. When beech strikes back: How strict nature conservation reduces herb-layer diversity and productivity in Central European deciduous forests. *For. Ecol. Manag.* **2014**, *319*, 51–61. [CrossRef]
39. Augusto, L.; Dupouey, J.; Ranger, J. Effects of tree species on understory vegetation and environmental conditions in temperate forests. *Ann. For. Sci.* **2003**, *60*, 823–831. [CrossRef]
40. Durak, T.; Holeksa, J. Biotic homogenisation and differentiation along a habitat gradient resulting from the ageing of manager beech stands. *For. Ecol. Manag.* **2015**, *351*, 47–56. [CrossRef]
41. Vacek, S.; Černý, T.; Vacek, Z.; Podrázský, V.; Mikeska, M.; Králíček, I. Long-term changes in vegetation annd site conditions in beech and spruce forest of lower mountains ranges of Central Europe. *For. Ecol. Manag.* **2017**, *398*, 75–90. [CrossRef]
42. Vacek, S.; Prokůpková, A.; Vacek, Z.; Bulušek, D.; Šimůnek, V.; Králíček, I.; Prausová, R.; Hájek, V. Growth response of mixed beech forests to climate change, various management and game pressure in Central Europe. *J. For. Sci.* **2019**, *65*, 331–345. [CrossRef]
43. Bosela, M.; Štefančík, I.; Petráš, R.; Vacek, S. The effects of climate Warming on the growth of European beech forest depend critically on thinning strategy and site productivity. *Agric. For. Meteorol.* **2016**, *222*, 21–31. [CrossRef]
44. Krupková, L.; Havránková, K.; Krejza, J.; Sedlák, P.; Marek, M.V. Impact of water scarcity on spruce and beech forests. *J. For. Res.* **2019**, *30*, 899–909. [CrossRef]
45. Parpan, V.I.; Stojko, S.M.; Parpan, T.V. Phytocoenotical and ecological characterization of beech forests (*Fagus sylvaticae* L.) of Ukraine and possibility to expand their area due to global Warming. *Infrastruktura i Ekologia Terenów Wiejskich* **2013**, *2*, 29–44.
46. Melo, M.; Lapin, M.; Kapolková, H.; Pecho, J.; Kružicová, A. Climate Trends in the Slovak Part of the Carpathians. In *The Carpathians: Integrating Nature and Society Towards Sustainability. Environmental Science and Engineering*; Kozak, J., Ostapowicz, K., Bytnerowicz, A., Wyżga, B., Eds.; Springer: Berlin/Heidelberg, Germany, 2013; pp. 131–150. [CrossRef]
47. Henrichs, S.; Winterhoff, W.; Schmidt, W. Vegetation dynamics of beech forests on limestone in central Germany over half a century–Effects of climate change, forest management, eutrophication or game browsing? *Biodivers. Ecol.* **2012**, *4*, 49–61. [CrossRef]
48. Zellweger, F.; De Frenne, P.; Lenoir, J.; Van Gansbeke, P.; Verheyen, K.; Bernhardt-Römermann, M.; Baeten, L.; Hédl, R.; Berki, I.; Brunet, J.; et al. Forest microclimate dynamics drive plant responses to Warming. *Science* **2020**, *368*, 772–775. [CrossRef]
49. Felsmann, K.; Baudis, M.; Kayler, Z.E.; Puhlmann, H.; Ulrich, A.; Gessler, A. Responses of the structure and function of the understory plant communities to preciptation reduction across forest ecosystems in Germany. *Ann. For. Sci.* **2018**, *75*, 3. [CrossRef]
50. Archaux, F.; Wolters, V. Impact of summer drought on forest biodiversity: Why do we know? *Ann. For. Sci.* **2006**, *63*, 645–652. [CrossRef]
51. Dzwonko, Z. Forest communities of the Gory Słonne Range (Polish Eastern Carpathians). *Fragm. Flor. Geobot.* **1977**, *23*, 161–200.
52. Skiba, S.; Drewnik, M. Soil map of the polish carpathian mountains. *Rocz. Bieszcz.* **2003**, *11*, 15–20.
53. Meteorological Data. Averages and Monthly Totals. Lesko. Available online: https://meteomodel.pl (accessed on 16 March 2021).

54. Trampler, T.; Mąkosa, K.; Girżda, A.; Bąkowski, J.; Dmyterko, E. *Siedliskowe Podstawy Hodowli Lasu*; PWRiL: Warsaw, Poland, 1990. (In Polish)
55. CORINE land Cover-CLC. Available online: https://clc.gios.gov.pl (accessed on 16 March 2021).
56. Braun−Blanquet, J. *Pflanzensoziologie, Grundzüge der Vegetationskunde*; Springer: Vienna, Austria, 1964.
57. Thom, D.; Sommerfeld, A.; Sebald, J.; Hagge, J.; Müller, J.; Seidl, R. Effect of disturbance patterns and deadwood on the microclimate in European beech forests. *Agric. For. Meteorol.* **2020**, *291*, 108066. [CrossRef]
58. Ewald, J.; Jehl, H.; Braun, L.; Lohberger, E. Die Vagetation des Nationalparks Bayerischer Wald als Ausdruck von Standort und Walddynarnik. *Tuexenia* **2011**, *31*, 9–38.
59. Hermy, M.; Honnay, O.; Firbank, L.; Grashof−Bokdam, C.; Lawesson, J.E. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biol. Conserv.* **1999**, *91*, 9–22. [CrossRef]
60. Dzwonko, Z.; Loster, S. Wskaźnikowe gatunki roślin starych lasów i ich znaczenie dla ochrony przyrody i kartografii roślinności. IGiPZ PAN. *Pr. Geogr.* **2001**, *178*, 120–132. (In Polish)
61. Matuszkiewicz, W. *Przewodnik do Oznaczania Zbiorowisk Roślinnych Polski. [A Guide for the Identification of Polish Plant Communities]*; Wydawnictwo Naukowe PWN: Warsaw, Poland, 2001. (In Polish)
62. Ellenberg, H.; Weber, H.E.; Düll, R.; Wirth, V.; Werner, W.; Paulissen, D. Zeigerwerte von Pflanzenin Mitteleuropa. *Scripta Geobot.* **1992**, *18*, 1–248.
63. Diekmann, M. Species indicator values as an important tool in applied plant ecology a review. *Basic Appl. Ecol.* **2003**, *4*, 493–506. [CrossRef]
64. Dufrene, M.; Legendre, P. Species assemblages and indicator species: The need for a flexible asymmetrical approach. *Ecol. Monogr.* **1997**, *67*, 345–366. [CrossRef]
65. Hammer, O.; Harper, D.A.T.; Ryan, P.D. PAST: Paleontological statistics software package for education and data analysis. *Palaeontol. Electron.* **2001**, *4*, 1–9.
66. Rozkrut, D. *Roczniki Statystyczne Leśnictwa 2020*; GUS: Warsaw, Poland, 2020. (In Polish)
67. MacDonald, D.; Crabtree, J.R.; Wiesinger, G.; Dax, T.; Stamou, N.; Fleury, P.; Lazpita, J.G.; Gibon, A. Agricultural abandonment in mountain areas of Europe: Environmental consequences and policy response. *J. Environ. Manage.* **2000**, *59*, 47–69. [CrossRef]
68. Kozak, J.; Estreguil, C.; Troll, M. Forest cover changes in the northern Carpathians in the 20th century: A slow transition. *J. Land Use Sci.* **2007**, *2*, 127–146. [CrossRef]
69. Kozak, J. Forest Cover Changes and Their Drivers in the Polish Carpathian Mountains since 1800. In *Reforesting Landscapes Linking Pattern and Process*; Nagendra, H., Southworth, J., Eds.; Springer: Dordrecht, The Netherlands; Heidelberg, Germany; London, UK; New York, NY, USA, 2010; pp. 253–273. [CrossRef]
70. Kozak, J.; Szwagrzyk, M. Have there been forest transitions? Forest transition theory revisited in the context of the Modifiable Areal Unit Problem. *R. Geogr. Soc. IBG* **2016**, *48*, 504–512. [CrossRef]
71. Bugno-Pogoda, A.; Durak, R.; Durak, T. Impact of Forest Management on the Temporal Dynamics of Herbaceous Plant Diversity in the Carpathian Beech Forests over 40 Years. *Biology* **2021**, *10*, 406. [CrossRef] [PubMed]
72. Ujházy, K.; Hederová, L.; Máliš, F.; Ujházyová, M.; Bosela, M.; Čiliak, M. Overstorey dynamics controls plant diversity in age-class temperate forests. *For. Ecol. Manag.* **2017**, *391*, 96–105. [CrossRef]
73. Schütz, J.P. Silvicultural tools to develop irregular and diverse forest structures. *Forestry* **2002**, *75*, 329–337. [CrossRef]
74. Raymond, P.; Bedard, S.; Roy, V.; Larouche, C.; Tremblay, S. The irregular shelterwood system: Review, classification, and potential application to forests affected by partial disturbances. *J. For.* **2009**, *107*, 405–413.
75. Langenbruch, C.; Helfrich, M.; Flessa, H. Effects of beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*) and lime (*Tilia spec.*) on soil chemical properties in a mixed deciduous forest. *Plant Soil.* **2012**, *352*, 389–403. [CrossRef]
76. Facelli, J.M.; Pickett, S.T.A. Plant litter: Its dynamics and effects on plant community structure. *Bot. Rev.* **1991**, *57*, 1–32. [CrossRef]
77. Depauw, L.; Perring, M.P.; Landuyt, D.; Maes, S.L.; Blondeel, H.; De Lombaerde, E.; Brūmelis, G.; Brunet, J.; Closset-Kopp, D.; Czerepko, J.; et al. Light availability and land-use history drive biodiversity and functional changes in forest herb layer communities. *J. Ecol.* **2019**, *108*, 1411–1425. [CrossRef]
78. Bergstedt, J.; Hagner, M.; Milberg, P. Effects on vegetation composition of a modified forest harvesting and propagation method compared with clear-cutting, scarification and planting. *Appl. Veg. Sci.* **2008**, *11*, 159–168. [CrossRef]
79. Durak, T.; Bugno-Pogoda, A.; Durak, R. Application of forest inventories to assess the forest developmental stages on plots dedicated to long-term vegetation studies. *For. Ecol. Manag.* **2021**, *489*, 119041. [CrossRef]
80. Keenan, R.J. Climate change impacts and adaptation in forest management: A review. *Ann. For. Sci.* **2015**, *72*, 145–167. [CrossRef]
81. Kovács, B.; Tinya, F.; Ódor, P. Stand structural drivers of microclimate in mature temperate mixed forests. *Agric. For. Meteorol.* **2017**, *234–235*, 11–21. [CrossRef]

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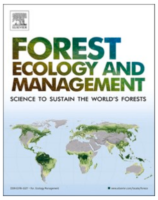

Impact of forest stand development on long-term changes in the herb layer of semi-natural Carpathian beech forests

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ABSTRACT

The distinction of changes in herb layer communities related to the dynamics of the forest stand and / or the regimes of forest management from that managed by random or non-random, global environmental disturbance, would allow for more precise recognition, and counteracting the effects of contemporary threats. In this work, we integrated databases of long-term vegetation records from tree research periods and archival forest inventory datasets to examine the changes in forest herb layer communities over time intervals of up to five decades across the major mountain forest habitat in the Polish Eastern Carpathians (managed semi-natural fertile mountain beech forests). Over the past half – century, these forests have been gradually aging. In this work, based on long-term datasets, we found clear differences in herb layer composition and diversity between beech forest developmental stages. Herb layer characteristics were compared between three forest stages, classified as broadly defined Growing (G), Optimum (O), and Terminal (T) stage. Stands in the Growing stage had the largest stocking, as well as the smallest volume, tree DBH and high, and age. Stands in the Optimum stage had the largest volume and tree height. Stands in the Terminal stage had the smallest stocking and the largest tree DBH and age. Although in the Optimum stage, the lowest beta diversity was recorded, this stage provided the best habitat conditions for species important from a beech forest's conservation status point of view (e.g. diagnostic for beech forests, ancient forest species). Moreover, in this stage the highest alpha diversity was recorded. We found that in gradually aging Carpathian forests the changes in the structure of stands play a significant role in controlling herb vegetation composition and diversity. The cause was the dominance of single developmental stages during temporally synchronous forest development in the studied region of the Carpathians over the past half – century (i.e. G in the 1970s, O in the 2000s and T in 2010s). Our results have important implications for forest management and biodiversity conservation. In particular, forest managers should ensure the creation and maintenance of forest landscapes with a more even share of development stages (mosaic of different age-classes). Additionally, this age differentiation of stands should be planned not on a local scale but on a regional scale.

1. Introduction

Herb layer plays a special role in the functioning of the forest ecosystem (Gilliam, 2007). It strongly influences the circulation of carbon and nutrients, and competitive interactions exert an impact on overstorey species' regeneration. Moreover, among forest strata, the herb layer has the highest plant diversity and as such is largely responsible for forest biodiversity (Gilliam, 2007; Landuyt et al., 2019). Despite being of significant importance, the herb layer is still underestimated by forest managers who, except for legally protected species, most often do not strive for its conservation. Therefore, there is a real need to gather solid knowledge of factors and mechanisms shaping forest herb communities. Based on this, forest management could be improved to support herb community conservation action plans. Nowadays, it is a very important issue, as we are dealing with rapid changes in the natural species composition of forest plant communities, which threaten the functioning of entire ecosystems (Rackham, 2008; Hessburg et al., 2019; McDowell et al., 2020).

The works analysing the archival records of European forest vegetation, emphasises, the great importance of several external drivers of temporal changes, leading to significant changes in forest environments, and thus plant communities, since the second half of the 20th century.

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The main drivers managing these changes, above all, include climate change (Milad et al., 2011), air pollution (Steubing et al., 1989; Schmitz et al., 2019), land use change (Verheyen et al., 2003) herbivore pressure (Rooney, 2009) and forest management or non-commercial use of forests by humans (Bürgi et al., 2013; Durak and Durak, 2016; Perring et al., 2018). However, in addition to external causes mentioned above, changes in forest plant communities are the result of more endogenous causes resulting from the natural dynamics (life cycle) of the forest, or cyclical forest regeneration (Korpel, 1995; Meyer, 1999; Standovár and Kenders, 2003). Moreover, due to the longevity of forest phytocoenoses (life cycle takes approximately 230 years in unmanaged and c.a. 120 years in managed beech forests (Korpel, 1995; Banaś et al., 2014; Bugno-Pogoda et al., 2021), cyclical changes in forest plant communities may interfere with changes of a global nature, making it difficult to identify the real causes of changes and their mechanisms. Although interactions between herb and overstorey layers have been well documented (Gilliam et al., 1995, Gilliam and Roberts, 2003), as far as we know, studies examining the impact of the dynamics of a European temperate forest on herb plant communities are scarce (Ujházy et al., 2005, 2017; Šamonil and Vrška, 2007; Vacek et al., 2017) and are often made using chrono-sequences (Ujházy et al., 2005, 2017). However, if we want to explain temporal changes in forest understorey species, chrono-sequences cannot accurately explain it (De Lombaerde et al., 2018).

Previous works have shown the existence of the influence of forest development stages on the forest herb layer characteristics. These dependencies were smaller in the case of natural beech forests than in the managed forest (Ujházy et al., 2005, 2017). On the other hand, Vacek et al. (2017) when examining temporal changes in herb layer characteristics, suggested rather conservative dependency with developmental stages in managed beech forests. Overstorey tree competition (expressed by stand density and age) was found as the most important driver of herb layer composition, diversity and dynamics (Ujházy et al., 2017). Also Ujházy et al. (2005) stressed high importance on the density of understorey trees in limiting the development of the herb layer. It is also known that the relationship between herb and overstorey layers in natural beech and fir forests is the strongest in the optimum stage and the weakest in the terminal stage (Šamonil and Vrška, 2007). Moreover, along with the development of these stands (in later stages of development), soil trophism and pH increase (Šamonil and Vrška, 2007), which has not been confirmed so far for managed forests.

In this work, we undertook an assessment of the forest stand dynamics and its impact on temporal changes in herb layer characteristics in semi-natural ageing Carpathian beech forests, based on long-term vegetation records. Moreover, we present the usefulness of the previously proposed method (Durak et al., 2021) for distinguishing forest developmental stages, based on archival forest inventories. The aim of the work was: (1) evaluate the utility of the method adopted from Durak et al. (2021) for identification of forest developmental stages for long-term vegetation records (1970s, 2000s and 2010s), (2) an assessment of the differences in herb layer species' composition and diversity between developmental stages. Additionally, this study addresses question (3) the impact of changes in the developmental stages of the Carpathian fertile beech forests on temporal changes in herb layer, and the implications for future forest management strategies.

2. Material and methods

2.1. Study site

The study area was located in the Sanocko-Turczańskie Mountains and a small neighbouring fragment of the Dynowskie Foothills in the Polish Eastern Carpathians (with the centre coordinates: 49°33′6″ N; 22°20′42″ E; Fig. 1). Elevation varies from 420 m a.s.l. to 652 m a.s.l. The forests in this area are mostly self-regenerating protective forests

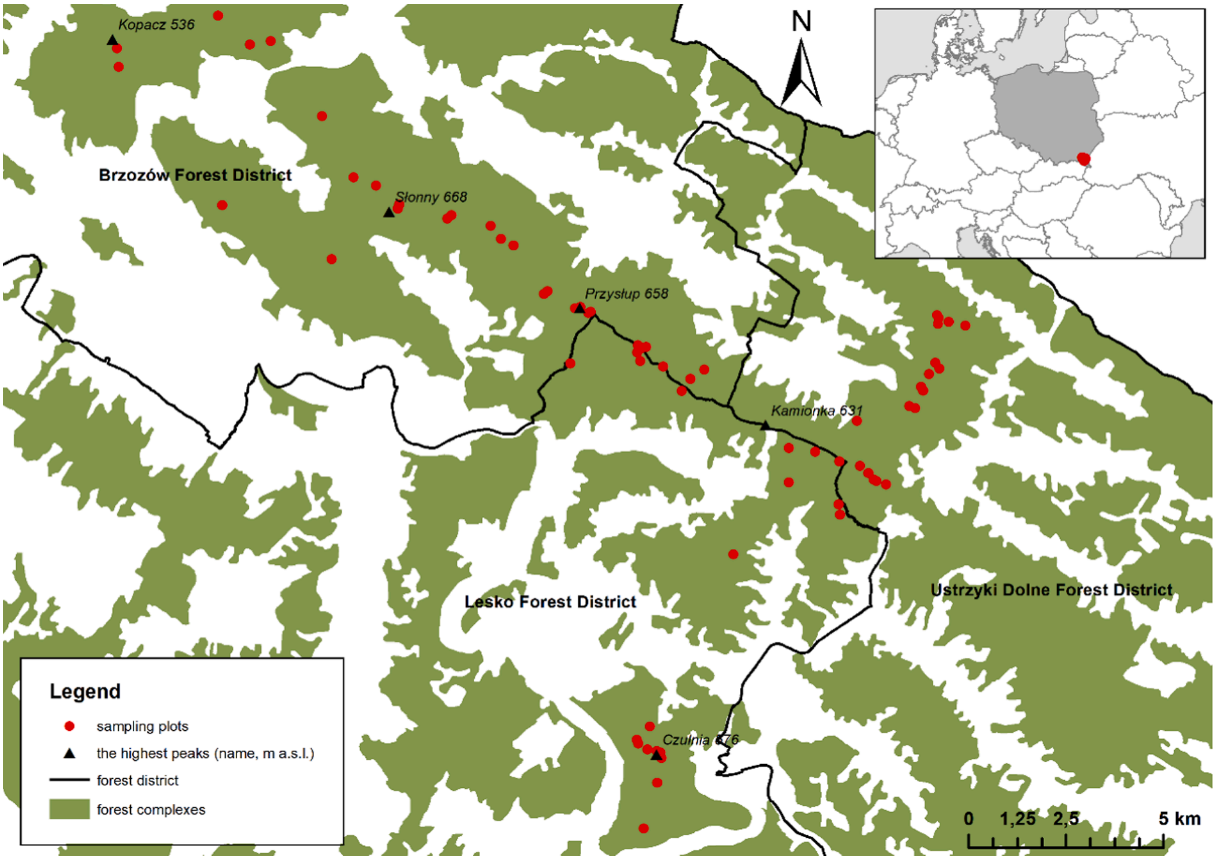

Fig. 1. Location of the study site and distribution of sampling plots within the area.

managed by Forest Districts - Brzozów, Lesko and Ustrzyki Dolne. Between the 1950s and 1990s the forests were regenerated using the uniform shelterwood system. At the end of the 1990s, the management system was changed to an irregular shelterwood system. This method of management is characterised by an extended rotation age (100–130 years) and long period of regeneration (from 30 to 50 years) (for more details, please see Bugno-Pogoda et al., 2021). The age-class structure and dominant species of forest stands changed significantly from the 1970s to 2010s (Fig. A1). In the 1970s, forests in the 21–40-year age-class dominated and mean stand age was 85 years. Within 40 years, the share of forests in the older age classes increased and decreased in the younger age classes and mean stand age reached 113 years (Bugno-Pogoda and Durak, 2021). According to Forest Management Plans from the 2010s, the average cut size is 4.5 and 8.6 m^3 / 1 ha / year for tree thinning and harvesting, respectively. The dominant plant community was *Dentario glandulosae Fagetum* Klika 1927 em. Mat. 1964, composed of the following units *D.g.-F. festucetosum drymei*, *D.g.-F. typicum*, *D.g.-F. lunarietosum*, *D.g.-F. allietosum ursinii* (Dzwonko, 1977). The stand in this plant community was dominated by *Fagus sylvatica* with admixture, mainly *Abies alba*, *Acer pseudoplatanus* and *Fraxinus excelsior*. The shrub layer is dominated by *F. sylvatica* (Bugno-Pogoda et al., 2021). Herb layer is dominated by *Anemone nemorosa, Dentaria bulbifera, Galium odoratum, Galeobdolon luteum, Oxalis acetosella, Mercurialis perennis* and *Athyrium filix-femina* (Dzwonko, 1977). From a phytosociological point of view, the diagnostic species are *Dentaria glandulosa*, *Polystichum braunii*, *Symphytum cordatum*, *S. tuberosum*, *Euphorbia amygdaloides*, *Glechoma hirsute* and *Salvia glutinosa* (Matuszkiewicz, 2001). This forest evolved mostly on acidic brown soils i.e. Eutric Cambisols, formed from Carpathian flysch (Dzwonko, 1977; Skiba and Drewnik, 2003). The mean annual temperature was 7.7 °C (and ranged from 6.0 to 9.3 °C), and the annual rainfall was 820.8 mm and ranged from 606.0 to 1104.2 mm (for the period 1966–2018; data from the meteorology station in Lesko − 420 m a.s.l. (Meteorological Data, 2021)). This area is part of the Natura 2000 network ("Ostoja Góry Słonne" PLH180013, for the protection of fertile mountain beech forest – habitat, code 9130), which includes the Słonne Mountains Landscape Park.

2.2. Data collection

An area of well-preserved managed semi-natural fertile mountain beech forests, covered with a network of 67 semi-permanent sampling plots devoted for long-term vegetation studies, was selected for data collection (Fig. 1, Durak and Holeksa, 2015). This network of plots was created on the basis of the first phytosociological description of these forests made in 1972–1973 by Professor Dzwonko (1977). Resurveys made by the authors in 2005–2007, and 2017–2018, allowed for the preparation of three vegetation records (henceforth 1970s, 2000s and 2010s; 201 records in total). Vegetation records were made using the Braun–Blanquet method (Braun-Blanquet, 1964) and saved in the form of so-called phytosociological relevés. Details on the re-localisation of plots and making phytosociological relevés were included in previous works (please see: Durak et al., 2021; Bugno-Pogoda et al., 2021).

As proposed by Durak et al. (2021), a set of stand variables, commonly available in archival Forest Management Plans (6 variables) and phytosociological relevés (4 variables) was used to identify developmental stages (Table A1). For this purpose, the variables included in phytosociological relevés from three research periods and forest management plans (by forest sub-compartments on which individual sampling plots were located) from time periods corresponding to vegetation research periods, were used. The plans prepared for the Forest Districts of the State Forests covering the area of the studied forests were used, i.e. Brzozów (as of 1976, 2007 and 2017), Lesko (as of 1976, 2009 and 2019) and Ustrzyki Dolne (as of 1977, 2009 and 2019).

2.3. Data analysis

2.3.1. Identification and characteristics of forest developmental stages

In order to identify the developmental stages of the stands in which the research plots were located in particular research periods, the method proposed by Durak et al. (2021) was used. Stand variables (listed in Table A1) from three study periods have been combined into one dataset. Before analyses, to improve the distribution and interpretability of data, datasets were square root transformed and standardised. To estimate the differences between the stand variables of recognised stages, a one-way ANOVA and Tukey's post-hoc test with Bonferroni correction was performed, and in the case of non-normal data distribution, a Kruskal – Wallis test followed by a Mann – Whitney *U* test with Bonferroni correction. To visualise and confirm the relationships between distinguished stages and stand characteristics assigned to sampling plots, discriminant analysis (LDA analysis; Xanthopoulos, et al., 2013), with group assignment cross-validated by a leave-one-out cross-validation (jackknifing) procedure, was performed. In order to visualise the dynamics of developmental stages, developmental stages on sampling plots in subsequent research periods were plotted. To confirm the difference in a stand's characteristics between developmental stages, a permutational multivariate analysis of variance (PerMANOVA analysis; Anderson, 2001), was done. The analysis was performed using of Gower distance, and the significance was assessed by permutation with 9,999 replicates. The significance of pairwise PerMANOVAs comparisons between stages, was estimated based on a post-hoc test with Bonferroni correction.

2.3.2. Impact of developmental stages on herb layer composition and diversity

To visualise shifts in composition of herb layer communities between developmental stages, non-metric multidimensional scaling analysis (NMDS, on two dimensions, using a Bray-Curtis distance measure), was performed. The significance of shifts along the first and second NMDS axes was indicated by a one-way ANOVA and Tukey's post-hoc test. To reveal the relationships between changes in herb layer composition represented by the NMDS axis scores and the herb layer characteristics, as well as stand variables, a Spearman rank correlation test was used.

Herb layer characteristics were analysed to delineate changes in species composition. We analysed groups of species distinguished based on traits, that are important for plant response to changes in the environment. Species richness (number of species) of the herb layer and their total coverage were calculated for each of 201 phytosociological relevés. In addition, analyses of the herb layer at development stages were carried out using characteristics obtained from ecological groups of species (list in Table 1), indicator species analysis and diversity indicators. The richness of groups of species with high or low habitat requirements was defined based on the Ellenberg indicator values (EIVs, Ellenberg et al., 1992; EIVs ≥ 7, L_H, F_H, R_H, and N_H and EIVs ≤ 3, L_L, R_L, and N_L). Because of the small number of eligible species, we did not evaluate the F_L group, and the T_L and T_H were expanded to involve species with indicator values ≤ 4 and ≥ 6, respectively. Beech forest species were defined as species diagnostic for fertile mountain beech forests from a phytosociological point of view (diagnostic species of association *Dentario glandulosae-Fagetum* and alliance *Fagion sylvaticae*, according to Matuszkiewicz, 2001). These species were treated as indicators of the conservation status of the fertile mountain beech forests. Ancient forest species (indicators of long-term site stability) were identified from Hermy et al. (1999), and Dzwonko and Loster (2001). Nitrophilous plant species were defined as herb species diagnostic of alliance *Atropetalia* and class *Epilobietea angustifolii*, according to Matuszkiewicz (2001). Fast-dispersing plant species (including anemochores, endozoochores and epizoochores) and slow-dispersing plant species (including myrmecochores, hydrochores, baro- and autochores) were classified according to Hermy et al. (1999), and Dzwonko and Loster (2001).

To reveal a particular strategy of herb plant communities in

Table 1

Correlation between herb layer characteristics and NMDS axes (from Fig. 4) that represent variation of the herb species composition among the sampling plots from all research periods. ("+" and "−" symbols denote positive or negative trend, respectively; Spearman rank correlation test). Moreover, differences in herb layer characteristics between distinguished forest stages and research periods are presented. Differences were tested by main effects ANOVA and Tukey's post-hoc test. If the assumptions of this test were not met, Kruskal–Wallis test followed by a Mann–Whitney *U* test were used. Values with the same letter do not differ significantly ($p > 0.05$). F and ^{x}H (Chi^{2})—main effects ANOVA and Friedman test score, respectively. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$. L, T, F, R, and N with L or H subscript: richness of groups of species with high or low habitat requirements for light, temperature, moisture, reaction, and nitrogen, defined based on the Ellenberg indicator values.

	Abbreviation	Spearman's correlation		Differences between stages represented by mean (±SE) values				Differences between research periods represented by mean (±SE) values (partially based on Bugno-Pogoda et al. 2021, Bugno-Pogoda and Durak 2021)			
		NMDS 1	NMDS 2	Test score: F lub H	Growing (G)	Optimum (O)	Terminal (T)	Test score: F lub ^{x}H	1970s	2000s	2010s
No. of species	N_Sp	ns	− *	5.6**	23.6 1.3)^{a}	27.9 (0.8)^{b}	23.7 (1.2)^{a}	31.0***	27.9 (1.0)^{a}	30.2 (1.0)^{a}	20.1 (0.7)^{b}
Total cover of species	Cov_Sp	+ **	+ ***	^{x}11.6**	81.9 (6.6)^{a}	105.3 (3.7)^{b}	115.4 (8.0)^{b}	^{x}25.3***	86.1 (4.5)^{a}	98.1 (3.8)^{b}	128.7 (6.8)^{b}
No. of beech forest species	N_Sp_bee	+ ***	ns	5.3**	3.1 (0.2)^{a}	3.9 (0.1)^{b}	3.2 (0.2)^{a}	4.2*	3.9 (0.2)^{a}	3.7 (0.2)^{a}	3.1 (0.2)^{b}
No. of ancient forest species	N_Sp_anc	ns	− ***	4.4*	15.6 (0.8)^{a}	18.4 (0.6)^{b}	14.8 (0.9)^{a}	35.9***	18.7 (0.7)^{a}	20.0 (0.8)^{a}	12.3 (0.5)^{b}
No. of species associated with forest clearings	N_Sp_cle	− *	+ ***	2.5	1.5 (0.2)^{a}	1.5 (0.1)^{a}	1.8 (0.1)^{a}	2.3	1.4 (0.1)^{a}	1.8 (0.1)^{a}	1.6 (0.1)^{a}
Total cover of species associated with forest clearings	Cov_Sp_cle	ns	+ ***	^{x}35.4***	2.2 (0.7)^{a}	5.9 (1.2)^{a}	12.8 (2.0)^{b}	^{x}39.1***	1.2 (0.2)^{a}	9.1 (1.9)^{b}	10.8 (1.5)^{c}
No. of fast species	N_Sp_fas	ns	− *	3.1*	6.4 (0.4)^{ab}	7.2 (0.3)^{a}	5.9 (0.4)^{b}	36.7***	7.9 (0.4)^{a}	7.7 (0.4)^{a}	4.4 (0.2)^{b}
No. of slow species	N_Sp_slo	− ***	− **	^{x}8.8*	4.5 (0.4)^{ab}	4.9 (0.2)^{a}	3.8 (0.3)^{b}	^{x}49.0***	4.7 (0.2)^{a}	6.0 (0.3)^{b}	3.0 (0.2)^{c}
L_L	L_L	ns	− ***	2.7	8.0 (0.4)^{ab}	9.0 (0.3)^{a}	7.3 (0.4)^{b}	40.8***	8.9 (0.3)^{a}	10.1 (0.3)^{b}	6.2 (0.3)^{c}
L_H	L_H	ns	+ ***	3.1*	2.2 (0.2)^{a}	2.6 (0.1)^{ab}	3.0 (0.2)^{b}	1.6	2.4 (0.2)^{a}	2.8 (0.2)^{a}	2.7 (0.2)^{a}
T_L	T_L	ns	ns	^{x}1.7	1.7 (0.2)^{a}	2.0 (0.1)^{a}	2.0 (0.2)^{a}	^{x}21.7***	2.1 (0.2)^{a}	2.4 (0.2)^{a}	1.4 (0.1)^{b}
T_H	T_H	− ***	ns	2.1	1.7 (0.3)^{a}	1.6 (0.1)^{a}	1.9 (0.2)^{a}	2.2	1.6 (0.2)^{a}	1.9 (0.2)^{a}	1.6 (0.2)^{a}
F_H	F_H	+ ***	ns	^{x}7.8*	2.1 (0.2)^{a}	3.0 (0.2)^{b}	2.7 (0.2)^{ab}	^{x}43.6***	2.7 (0.2)^{a}	3.8 (0.2)^{b}	1.8 (0.2)^{c}
R_L	R_L	− ***	ns	^{x}3.5	0.4 (0.1)^{a}	0.3 (0.04)^{a}	0.4 (0.1)^{a}	^{x}3.1	0.2 (0.1)^{a}	0.4 (0.1)^{a}	0.3 (0.1)^{a}
R_H	R_H	+ ***	− *	7.9***	7.6 (0.6)^{a}	10.3 (0.4)^{b}	8.3 (0.5)^{a}	16.4***	10.4 (0.5)^{a}	10.5 (0.5)^{a}	7.0 (0.4)^{b}
N_L	N_L	− ***	ns	0.5	0.4 (0.1)^{a}	0.4 (0.1)^{a}	0.4 (0.1)^{a}	0.6	0.4 (0.1)^{a}	0.4 (0.1)^{a}	0.3 (0.1)^{a}
N_H	N_H	+ ***	ns	7.6***	7.4 (0.7)^{a}	10.1 (0.4)^{b}	8.4 (0.6)^{a}	15.9***	9.7 (0.5)^{a}	10.7 (0.6)^{a}	7.0 (0.4)^{b}
Herb's strategy C (%)	C_herb	+ ***	− ***	3.6*	38.5 (0.7)^{ab}	40.0 (0.4)^{a}	38.0 (0.6)^{b}	12.8***	40.9 (0.5)^{a}	39.4 (0.5)^{a}	37.2 (0.5)^{b}
Herb's strategy S (%)	S_herb	− ***	+ ***	1.9	27.5 (1.2)^{a}	27.0 (0.5)^{a}	31.6 (1.2)^{b}	8.9***	25.9 (0.7)^{a}	27.0 (0.7)^{a}	31.9 (1.0)^{b}
Herb's strategy R (%)	R_herb	ns	ns	^{x}1.4	48.6 (0.8)^{a}	48.5 (0.3)^{a}	48.1 (0.4)^{a}	^{x}0.2	48.7 (0.4)^{a}	48.5 (0.3)^{a}	48.1 (0.5)^{a}
Seedling's strategy C (%)	C_seed	+ *	+ ***	^{x}3.0	36.4 (1.6)^{a}	39.8 (0.7)^{a}	37.8 (1.8)^{a}	^{x}7.9*	36.7 (1.1)^{a}	40.2 (0.7)^{b}	39.1 (1.5)^{ab}
Seedling's strategy S (%)	S_seed	ns	ns	^{x}0.5	44.7 (1.9)^{a}	43.8 (0.8)^{a}	42.1 (2.2)^{a}	^{x}2.1	42.3 (1.4)^{a}	45.2 (0.9)^{a}	43.1 (1.8)^{a}
Seedling's strategy R (%)	R_seed	ns	− ***	^{x}2.0	16.1 (0.9)^{a}	15.3 (0.5)^{a}	14.3 (0.9)^{a}	^{x}23.7***	17.6 (0.7)^{a}	14.6 (0.4)^{b}	13.4 (0.7)^{b}
Shannon index	Sh_Div	ns	ns	5.9**	2.8 (0.1)^{a}	3.0 (0.03)^{b}	2.9 (0.1)^{ab}	11.9***	3.0 (0.05)^{a}	3.0 (0.04)^{a}	2.8 (0.04)^{b}
Evenness	Even	ns	+ ***	^{x}25.3***	0.7 (0.02)^{a}	0.7 (0.01)^{a}	0.8 (0.01)^{b}	^{x}58.4***	0.7 (0.01)^{a}	0.7 (0.01)^{a}	0.8 (0.01)^{b}

developmental stages, the C-S-R (competitor, stress tolerator and ruderal plant strategies) model of Grime (1977, 2001) was applied. As was shown in previous works, an average C-S-R plant strategy for plant communities can be applied to obtain a "functional signature" (summary) for vegetation (Hunt et al., 2004, Caccianiga et al., 2006, Pierce et al., 2013). Here we compared the share of three primary plant strategies (C, S and R) between developmental stages. For this purpose we computed the average percentage of these strategies for each of 201 phytosociological relevés from the 1970s to the 2010s based on plant species CSR strategy data (i.e. C, S, R percentages) provided by Pierce et al. (2017). Because the functional signal of woody species exhibit a much shorter range of strategies (ruderal tree species are rare) than herb species, to obtain a reliable outcome, we conducted two separate analyses.

For a better understanding of the relationships between herb layer communities and particular forest developmental stages, we identified species, indicative for a given developmental stage, by applying an indicator species analysis (IndVal, Dufrêne and Legendre, 1997). We used data for plant species with a total attendance of at least 5%. The statistical significance of the species indicator values (IndVal) was estimated by 9,999 random permutations. We anticipated that the ecological requirements of received groups of indicator species would allow for the identification of the main drivers managed by the herb vegetation during the forest management cycle.

To recognise the herb layer diversity of the particular developmental stages we considered alpha (Shannon and evenness diversity indices) and beta (expressed by Simpson dissimilarity index that describes spatial species turnover (Simpson, 1943, Baselga, 2010)) diversities. To detect the processes of biotic homogenisation or differentiation during forest development, we applied a method based on the average inter-plot dissimilarities (Rooney et al., 2004; Van Calster et al., 2007; Durak et al., 2015). Changes in plant diversity were computed as the difference in the pairwise species' dissimilarities between the particular developmental stages (Olden and Poff, 2003). To achieve this, a Simpson dissimilarity index was calculated, for all possible pairs of phytosociological relevés, for the G, O and T stage. Then, the average dissimilarity indices were calculated for each vegetation record classified to one of the developmental stages. Differences between the stages were assessed by a one-way ANOVA and Tukey's post-hoc test. We made an assumption that decreases in the mean values of the Simpson index could indicate the herb layer homogenisation during a change in the forest developmental stage, otherwise differentiation.

To estimate the differences between the herb layer characteristics among recognised stages and research periods, a main effects ANOVA and Tukey's post-hoc test with Bonferroni correction, and in the cases of non-normal data distribution, a Kruskal–Wallis test followed by a Mann–Whitney *U* test with Bonferroni correction, were performed. To confirm the difference in composition of herb layer communities between developmental stages and research periods, a PerMANOVA analysis (Anderson, 2001), was done. The analysis was performed with Bray-Curtis distances, and the significance was assessed by permutation with 9,999 replicates. The significance of pairwise PerMANOVA comparisons, was estimated based on a post-hoc test with Bonferroni correction.

2.3.3. *Vegetation data handling*

Before statistical analyses, abundance data estimated by the Braun-Blanquet cover-abundance scale, were converted to respective mid-point percentage values. Then, to improve the normality of distribution, data were square root-transformed. All species recorded in the herb layer, except rarely encountered early spring geophytes (which flower from February to April and have short-lived aboveground shoots, e.g. *Adoxa moschatellina* or *Galanthus nivalis*), were included in the univariate analyses. In the case of multivariate analyses, species with a total frequency of <5% were excluded from the pool of species. To eliminate errors resulting from misidentification of similar species, *Senecio fuchsii* and *S. nemorensis* were assigned into one group (*Senecio* sp.). The same was applied to ferns of the genus *Dryopteris*. Species nomenclature was used following Mirek et al. (2002). Statistical analyses were calculated using PAST software package 4.0 (Hammer et al., 2001). Main effects ANOVA analysis was performed using TIBCO Statistica 13 software.

3. Results

3.1. *Dynamics of developmental stages*

Based on a method proposed by Durak et al. (2021), in every research period, three broadly defined forest developmental stages were distinguished and characterised: Growing (G), Optimum (O), and Terminal (T) stage (Table 2, Figs. 2 and A2). These stages corresponded to those identified by Durak et al. (2021). Despite some differences resulting from tree harvesting, stages showed high compliance with those described in old-growth forests (Table A2; Durak et al. 2021). The similarity was especially visible in the case of such stand variables as tree height and DBH, and stocking. The dynamics of tree volume was also similar, but in managed forests (especially in the terminal stage) the values were lower. Similarly, the age of the last developmental stage was lower than in old-forests, which was a consequence of forest management (Table A2).

Table 2
Difference in composition of considered stand variables between distinguished forest stages. Different letters in the same row indicate that groups are statistically different at $p \leq 0.05$ (based on PerMANOVA analysis with post-hoc test).

	Test score (F)	Comparisons between stages		
		G	O	T
Forest stages in the 1970s	18.3***	a	b	c
Forest stages in the 2000s	22.2***	a	b	c
Forest stages in the 2010s	26.1***	a	b	c
Forest stages 1970–2010s	45.24***	a	b	c

*** $p \leq 0.001$.

Generally, considering stand variables from forest inventories (Management Plans), the distinguished stages differed in terms of Stocking (the highest in G and the lowest in T) as well as Tree_H_Inv, Tree_DBH_Inv and Age-class or Age, which were lowest in G. Additionally, considering variables measured in the sampling plot, developmental stages differed in Tree_Cov and Total_Cov (the lowest in T) as well as Shrub_Sam, which was the lowest in G and the highest in T (Table 3).

In each research period, the stands in the growing stage had on average the largest Stocking, as well as the smallest Tree_DBH_Inv, Tree_H_Inv and Age. The stands in the Optimum stage had the largest Volume on average (except in the 2000s, when it was similar for the G and O stages). As their Age was intermediate between the G and T stages, also most of the stand variables from forest management plans had intermediate values (e.g. Stocking, Tree_DBH_Inv, Tree_H_Inv). At the same time, the height of the trees measured on the plots was highest in the Optimum stage. In each research period, the stands at the Terminal stage had generally, the smallest Stocking, Tree_ Cov and Total_ Cov as well as the largest Tree_DBH_Inv and Age (Table 3).

Although the G, O and T developmental stages were distinguished in each of the research periods, their proportion changed over time. In the 1970s, apart O stage, the G stage was well represented (40 and 22 sampling plots, respectively). In the 2000s, most plots previously included in the G stage passed to the clearly dominant in this research period O stage (47 plots). Additionally, a few plots previously belonging to the O stage passed to the developing T stage. In 2010, a large part of the sampling plots that previously represented the O stage, passed to the dominant T stage, in this study period (36 sampling plots). As a result, the number of plots belonging to the O stage, decreased by almost half. Moreover, the G stage almost completely disappeared in the 2010s (Fig. 3).

During the 1970s – 2020s period, forest stands were aging. As a consequence, not only the developmental stages of stands on the sampling plots changed, but also the stand variables of the development stages themselves. In particular, in the forest development stages of the 1970s, Stocking, Tree_H_Inv and Volume were found to be smaller than in the corresponding development stages of the 2000s and 2010s. Moreover, in the Terminal stage from the 2010s, Tree_Cov and Aver_Tre_H were found to be much smaller, as well as a much larger Shrub_Sam than in T stage in other research periods (Table 3).

3.2. *Impact of developmental stages on herb layer composition and diversity*

NMDS analysis of the herb layer species composition indicated differences between herb layer species composition of beech forest

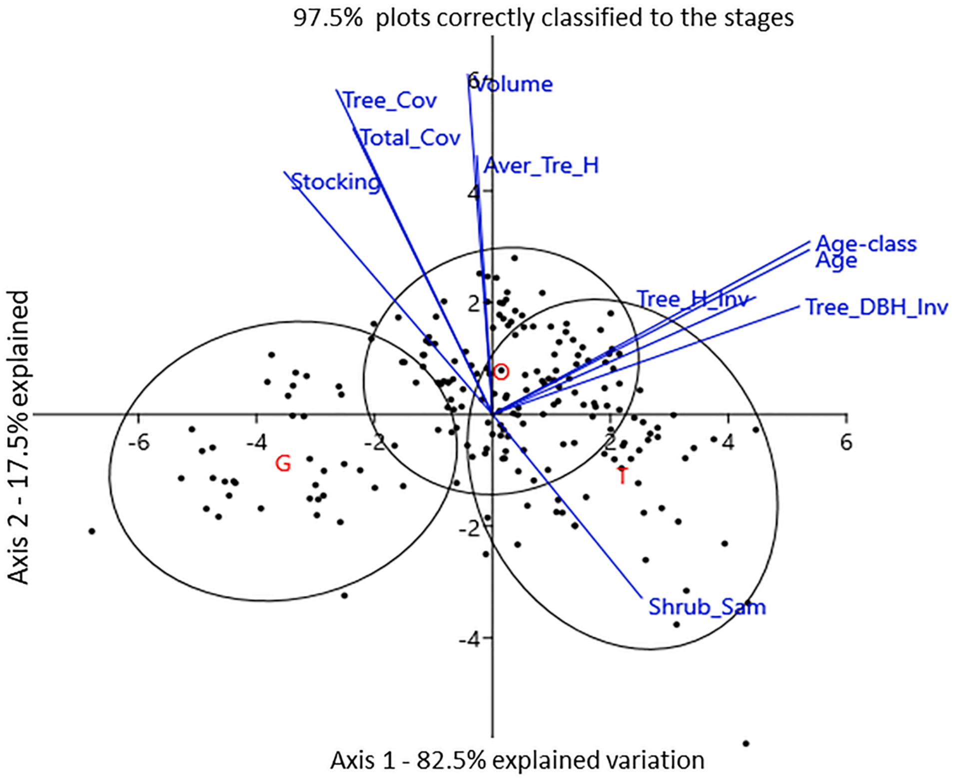

Fig. 2. Comparison of stand variables composition of forest stages determined by the LDA analysis based on combined data for the 1970s, 2000s and 2010s. The groups are marked with 95% ellipses. Variable abbreviations are explained in Table A1.

developmental stages (Fig. 4), as confirmed by PerMANOVA analysis ($F = 6.47$, $p < 0.001$, with significant differences ($p < 0.001$) between all stages according to a post-hoc test). The first and second NMDS axes expressed the impact of forest developmental stages on herb layer composition. This was supported by an ANOVA with post-hoc Tukey test showing that scores of NMDS1 and NMDS2 (represented herb vegetation of sampling plots) were significantly different among developmental stages. With regards to the first axis, stage G was different from the others. Considering the second NMDS axis, all stages were significantly different, with a high significance level (Table 4).

The correlation between NMDS axes and stand and herb layer variables/characteristics, revealed some gradients managing the changes in herb layer composition within stand development. The first NMDS axis was positively correlated with stand Age and Tree_DBH_Inv (Table A1). Moreover, it positively correlated with soil reaction, nitrogen and humidity and negatively with temperature on the forest floor (as demonstrated by groups of indicator species, Table 1). Along this axis, there is a notable increase in the number of beech forest species and the share of C - strategy component of herb species, and a decrease in the share of S - strategy component of herb species (Table 1). The second NMDS axis was strongly correlated with research period ($R = 0.67$, $p < 0.001$). Moreover, this axis was positively correlated with stand variables, such as Tree_DBH_Inv, Tree_H_Inv, Shrub_Sam and Age. Moreover, this axis was positively correlated with the amount of light on the forest floor (as demonstrated by groups of indicator species, Table 1). Along this axis, especially notable are the increased number and coverage of species associated with forest clearings, evenness and sum of plant species coverage, the share of S - strategy component of herb species and C - strategy component of seedlings. Moreover, a decreased number of ancient forest species, share of strategy C among herb and strategy R among seedling species (Table 1, A1).

Differences between herb layer composition among developmental stages were supported by an ANOVA / Kruskal-Wallis with posteriori tests in the case of most of the considered characteristics of the herb layer. Response of the herb layer to the change in the developmental stages showed linear (e.g. Cover of species associated with forest clearings, Evenness, Herb's strategy S%) or nonlinear (with highest values in Optimum stage, e.g. L_L, R_H, N_H) character. However, the latter dominated (Table 1).

Indicator species for the G stage had low light and soil nutrient requirements (e.g. *Lathyrus vernus*, *Luzula pilosa* and *Polygonatum multiflorum*). C-S-R signature of this group is characterised by dominance of R (average over 55%) as well as C (average 40%) components. The habitat requirements of the indicator species for the O stage were greater than for the G stage. Predominant among them were ancient forest species requiring average light conditions (ranging between shade and partial shade) and moderately rich and nutrient-rich soils (e.g. *Actaea spicata*, *Dentaria bulbifera*, *Lunaria rediviva*, *Pulmonaria obscura* and *Stellaria nemorum*). C-S-R signature of this group was dominated by C and R components. Their share was more even than in the G stage (46% on average for C and R), and the share of the C-component was highest among the stages. The indicator species for the T stage was distinguished by the highest requirements for light availability and soil nutrients. This group was characterised by the participation of forest clearings and margins species (e.g. *Rubus hirtus*, *Senecio* sp., *Stachys sylvatica*, *Urtica dioica* and *Rumex obtusifolius*). In the C-S-R signature of this group of species the C and R component also dominates. However, compared to the indicator species for the G and O stages, the share of C-component declined and S-component rose (as the effect of the increase in the density and competition of shrubs) (Table A3, A4, Fig. 5).

The lowest beta diversity was recorded in the O stage (Fig. 6). At the same, in this stage the highest alpha diversity (species richness, Shannon index) was recorded (Table 1). Low beta diversity resulted from the high similarity in terms of species composition (low species turnover) between the sampling plots. The low species turnover rate in the O stage was due to the low level of disturbances and arisen habitat conditions, optimal for forest species. In the G and T stages, beta diversity was high as a result of the low similarity of species composition (high species

Table 3

Mean (±SE) values of stand variables for distinguished forest stages in particular research periods and whole period from 1970 to 2010s. For comparison, values of stand variables for particular research periods have been added. Depending on data distribution, differences were tested by one-way ANOVA and Tukey's post-hoc test or Kruskal–Wallis test followed by a Mann–Whitney *U* test. Values with the same letter do not differ significantly ($p > 0.05$). F and H (Chi^2)—ANOVA and Friedman test score, respectively. * $p \leq 0.05$, ** $p \leq 0.01$, *** $p \leq 0.001$.

		No. of plots	Variables and units									
			Stocking –	Tree_DBH_Inv cm	Tree_H_Inv m	Volume m^3/ha	Age-class age-classes	Age years	Tree_Cov %	Shrub_Sam %	Aver_Tre_H m	Total_Cov %
1970s												
Test score	H or ^{x}F		^{x}17.11***	^{x}49.27***	33.67***	6.56**	43.35***	43.35***	^{x}3.76*	^{x}2.38	^{x}5.09**	^{x}3.67*
Mean (±SE) values	Growing (G)	22	0.7 (0.03)^{a}	25.9 (1.22)^{a}	21.0 (0.97)^{a}	242.9 (20.91)^{a}	3.4 (0.14)^{a}	61.8 (3.13)^{a}	87.5 (1.91)^{ab}	3.7 (±0.47)^{a}	28.4 (0.69)^{a}	88.0 (1.84)^{ab}
	Optimum (O)	40	0.6 (0.02)^{a}	42.4 (1.32)^{b}	26.4 (0.23)^{b}	303.4 (12.43)^{b}	5.2 (0.07)^{b}	96.1 (1.59)^{b}	88.4 (1.18)^{a}	6.6 (±0.99)^{a}	31.5 (0.60)^{b}	89.1 (1.12)^{a}
	Terminal (T)	5	0.3 (0.06)^{b}	53.4 (3.93)^{c}	27.2 (0.97)^{b}	196.0 (40.20)^{a}	5.2 (0.20)^{b}	97.0 (5.61)^{b}	78.0 (3.74)^{b}	6.0 (±0.63)^{a}	29.0 (1.87)^{ab}	79.3 (3.51)^{b}
2000s												
Test score	H or ^{x}F		^{x}22.69***	^{x}43.60***	16.37***	^{x}14.47***	^{x}57.1***	^{x}62.67***	^{x}23.04***	^{x}2.02	^{x}15.46***	18.09***
Mean (±SE) values	Growing (G)	9	1.1 (0.05)^{a}	30.3 (2.22)^{a}	24.7 (1.50)^{a}	428.2 (21.48)^{a}	3.4 (0.24)^{a}	65.6 (4.96)^{a}	87.2 (2.78)^{a}	9.7 (6.39)^{a}	25.1 (1.63)^{a}	89.6 (1.63)^{a}
	Optimum (O)	47	0.8 (0.03)^{b}	51.5 (0.95)^{b}	30.4 (0.39)^{b}	423.5 (12.61)^{a}	6.0 (0.10)^{b}	111.8 (1.68)^{b}	86.6 (1.01)^{a}	7.4 (1.24)^{a}	31.4 (0.58)^{b}	87.8 (0.88)^{a}
	Terminal (T)	11	0.5 (0.06)^{c}	51.2 (2.53)^{b}	30.5 (0.47)^{b}	286.6 (26.10)^{b}	6.1 (0.25)^{b}	113.8 (4.02)^{b}	70.5 (2.65)^{b}	14.2 (4.92)^{a}	34.0 (0.80)^{b}	75.2 (2.39)^{b}
2010s												
Test score	H or ^{x}F		39.96***	^{x}53.49***	15.59***	^{x}18.39***	^{x}46.66***	^{x}64.62***	29.60***	^{x}2.48	5.45	23.24***
Mean (±SE) values	Growing (G)	6	1.0 (0.06)^{a}	29.3 (2.62)^{a}	24.2 (1.74)^{a}	371.3 (47.57)^{ab}	3.7 (0.21)^{a}	65.0 (2.58)^{a}	95.8 (2.01)^{a}	16.7 (9.10)^{a}	28.3 (2.11)^{a}	97.1 (1.54)^{a}
	Optimum (O)	25	0.8 (0.02)^{a}	51.5 (1.59)^{b}	31.3 (0.44)^{b}	449.3 (20.86)^{a}	6.0 (0.17)^{b}	112.8 (3.23)^{b}	91.0 (1.41)^{a}	21.3 (3.03)^{a}	30.4 (0.94)^{a}	93.0 (1.17)^{a}
	Terminal (T)	36	0.5 (0.03)^{b}	57.2 (1.05)^{c}	31.7 (0.22)^{b}	281.8 (16.69)^{b}	6.4 (0.12)^{c}	121.2 (1.90)^{c}	65.6 (3.69)^{b}	32.5 (4.34)^{a}	24.9 (1.56)^{a}	78.4 (2.62)^{b}
1970s-2010s												
Test score	H or ^{x}F		62.64***	^{x}162.1***	76.81***	33.25***	^{x}206.6***	^{x}199.3***	58.66***	37.4***	19.53***	34.22***
Mean (±SE) values	Growing (G)	37	0.9 (0.04)^{a}	27.6 (1.03)^{a}	22.4 (0.77)^{a}	310.6 (20.47)^{a}	3.4 (0.11)^{a}	63.2 (2.23)^{a}	88.8 (1.43)^{a}	7.3 (2.19)^{a}	27.6 (0.65)^{a}	89.9 (1.29)^{a}
	Optimum (O)	112	0.7 (0.02)^{b}	48.2 (0.82)^{b}	29.1 (0.29)^{b}	385.3 (10.15)^{b}	5.7 (0.07)^{b}	106.3 (1.34)^{b}	88.1 (0.69)^{a}	10.4 (1.09)^{b}	31.3 (0.38)^{b}	89.4 (0.62)^{a}
	Terminal (T)	52	0.5 (0.03)^{c}	55.6 (1.02)^{c}	31.0 (0.27)^{c}	274.6 (13.63)^{a}	6.3 (0.11)^{c}	117.3 (1.91)^{c}	67.8 (2.67)^{b}	26.1 (3.45)^{c}	27.2 (1.22)^{ab}	77.8 (1.90)^{b}
Test score	H or ^{x}F		14.03***	^{x}33.30***	^{x}60.08***	^{x}23.13***	^{x}30.52***	^{x}34.89***	6.39*	56.80***	17.61***	3.01
Mean (±SE) values	1970s	67	0.6 (0.02)^{a}	37.9 (1.43)^{a}	24.7 (0.48)^{a}	275.6 (11.28)^{a}	4.6 (0.13)^{a}	84.7 (2.47)^{a}	87.3 (1,02)^{a}	5.6 (0,63)^{a}	30.3 (0.47)^{a}	88.0 (0.97)^{a}
	2000s	67	0.8 (0.03)^{b}	48.5 (1.23)^{b}	29.6 (0.42)^{b}	401.0 (11.97)^{b}	5.6 (0.14)^{b}	105.7 (2.50)^{b}	84.0 (1,16)^{a}	8.8 (1.45)^{a}	31.0 (0.55)^{a}	86.0 (0.96)^{a}
	2010s	67	0.6 (0.03)^{a}	52.7 (1.28)^{b}	30.9 (0.36)^{b}	349.4 (15.64)^{c}	6.0 (0.13)^{b}	113.0 (2.49)^{b}	77.6 (2,60)^{a}	27.2 (2.77)^{b}	27.1 (0.73)^{b}	85.5 (1.74)^{a}

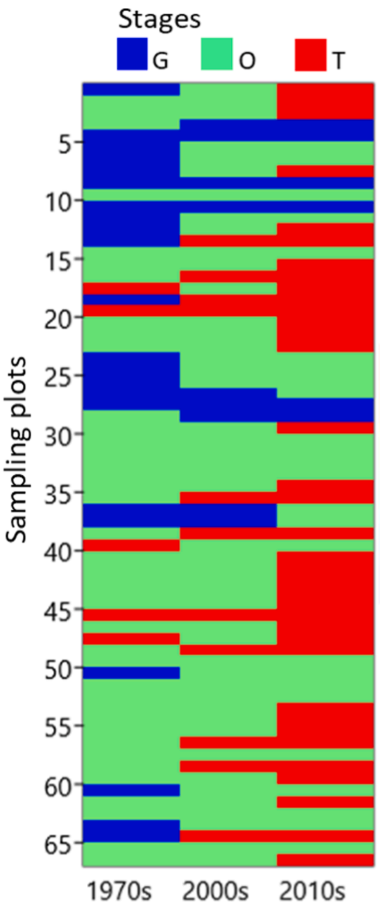

Fig. 3. Changes of the forest developmental stages on the corresponding sampling plots from subsequent research periods. Stacked bars represent the individual sampling plots classified into developmental stages according to the method of Durak et al. (2021).

turnover) between the plots. The high turnover rate of species was influenced by the high level of disturbances and the diversity of habitat conditions caused by non-commercial use (G stage) and the development of a new generation of trees (T stage) (Fig. 6). Results suggest biotic homogenisation of herb layer composition in the O stage.

3.3. *Changes in the herb layer composition between research periods*

NMDS analysis of the herb layer species composition indicated directional changes along second NMDS axis between the phytosociological relevés from subsequent research periods (Fig. 4), as confirmed by PerMANOVA analysis ($F = 11.71$, $p < 0.001$, with significant differences ($p < 0.001$) between all periods according to a post-hoc test). The differentiation of the herb layer characteristics between successive research periods often follows the change in the dominant developmental stage (Table 1). For example, in the 2000s and stage O, the highest number of species was recorded for: species on the sampling plot, ancient forest species, slow species and species with low light, and high trophic (L_L, N_H). Additionally, in the 2010s and stage T, the largest total cover of species associated with forest clearings and evenness was recorded, and the smallest number: species on the sampling plot, ancient forest species, slow species and species with low light, and high trophic (L_L, N_H).

4. Discussion

4.1. *Dynamics of developmental stages*

The method according to Durak et al. (2021) made it possible to identify three main developmental stages of the stand for the study plots in each of the research periods. The character of the stages were consistent with those previously reported from 2010s (Durak et al., 2021). Also, the consistent picture of transition between stages in subsequent research periods confirms the utility of this method for forest dynamics analysis, especially in the context of long-term vegetation studies.

Between the research periods, the stands in which the sampling plots were located became older and older (average age 85, 106, 113 years, successively). Although all three developmental stages were found in each research period, as a result of the transition between stages, the share of the G stage (max. in the 1970s) decreased and the proportion of the O (max. in the 2000s) and T stages (max. in the 2010s) increased with time. We found little variation in age and other stand variables, and a gradual shift from G to T stage over time. It follows that in each of the research periods, the structural differentiation of stands was small on a regional scale and determined by one of the developmental stages. Such small variability of forest stages on a regional scale has been identified as a threat contributing to the decrease in landscape-scale biodiversity (Schall et al., 2018).

4.2. *Impact of developmental stages on herb layer composition*

In stage G there were fast-growing young stands with a high stocking index. As was stressed by Cole and Rapp (1981), those young stands with high canopy closure are characterised by a high rate of nutrients uptake and simultaneously by a very low rate of nutrients uptake by ground vegetation. Moreover, in such a stand, the roots compete strongly for nutrients and water, limiting their availability to herb plants and acidifying the soil (Coomes and Grubb, 2000, Augusto et al., 2002, DeYoung, 2016). The lack of gaps in a dense beech stand (low light availability) and low soil moisture also reduced the rate of litter decomposition, causing its amount to be much greater than in the other stages (Barbier et al., 2008; Durak et al., 2021). The accumulating thick layer of beech litter additionally contributed to the lowering of the pH and concentrations of nutrients in the top layer of soil (Trap et al., 2011; Barbier et al. 2008), which resulted in the generation of a wide soil fertility, acidity and humidity gradient in the mountain forests (Fig. 4). This gradient contributed to the large variability in the species composition of the herb layer seen in the G stage. However, the best indicators were plant species of highly shaded and less fertile habitats: *Polygonatum multiflorum*, *Luzula pilosa* and *Festuca drymeia*.

In the optimum stage, gaps appeared in the stand as a result of the dying out of trees competing for resources and space, or forest treatments, and the growth rate of trees and the stocking index decreased. Moreover, tree roots competition for soil moisture and nutrients decreased (DeYoung, 2016), the amount of dead wood on the forest floor and the rate of decomposition of dead matter increased (Krishna and Mohan, 2017; Durak et al., 2021). As a consequence, the amount of nutrients and soil pH available to herb plants increased. An increase in the amount of light on the forest floor, the amount of nutrients in the soil and a moderate level of disturbances related to forest management at this developmental stage, created optimal development conditions for typical fertile mountain forest plants, including species diagnostic for the Carpathian beech forest (i.e. *Dentaria bulbifera*, *Lunaria rediviva*, *Symphytum cordatum*). This relationship of typical species of the Carpathian beech forest with the optimum stage confirms previous research results (Ujházy et al., 2005; Durak et al., 2021,).

In the T stage, the stocking index is the smallest, the tree cover is significantly reduced, and the amount of dead wood is the highest (Table 3, Durak et al., 2021). Apart from the more intensive cutting of

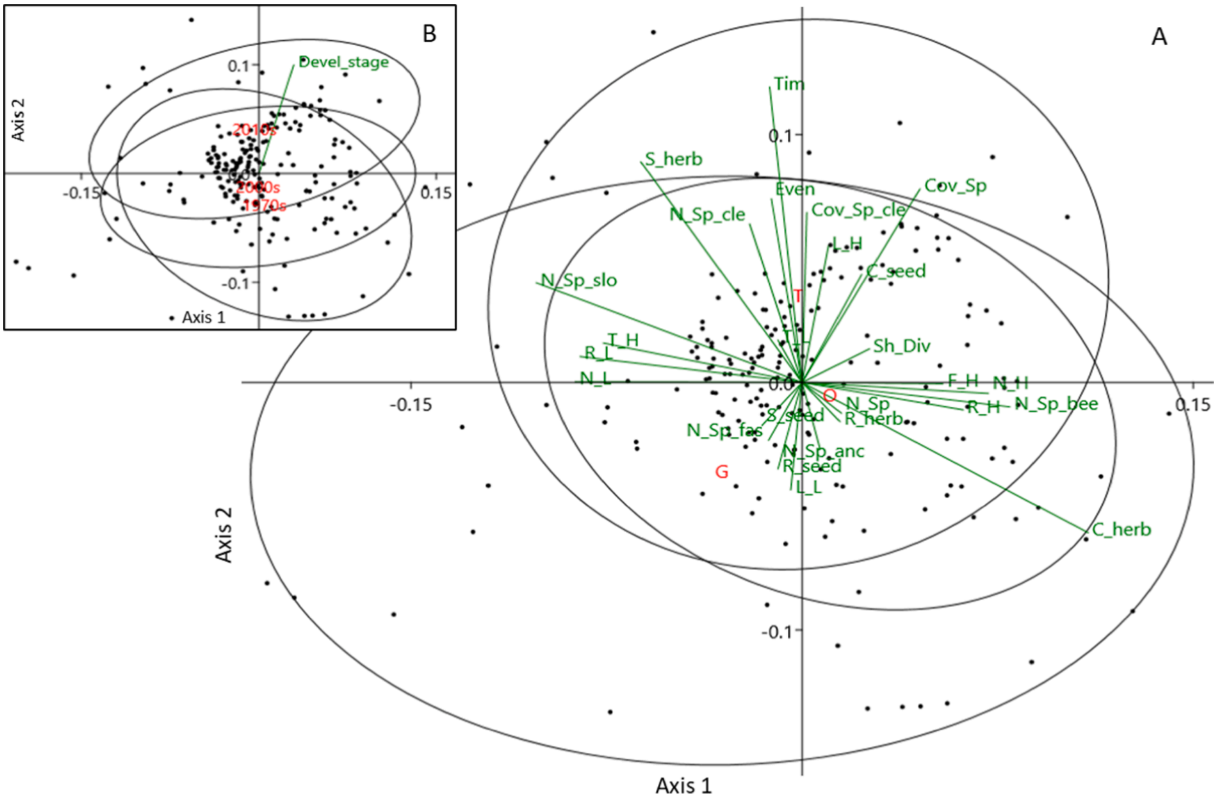

Fig. 4. Nonmetric multidimensional scaling diagram of the shift in herb layer composition between (A) the developmental stages (G, O and T) in the East Carpathian fertile beech forests and for the sake of comparison, between research periods (B). Vectors express the correlation of the herb layer characteristics with NMDS axes. The groups are marked with 95% ellipses. Herb layer characteristics abbreviations are explained in Table 1. Tim - research period (time), Dev_stage - developmental stage ranged from 1 to 3 for G, O and T).

Table 4
Difference in NMDS scores among distinguished developmental stages. Different letters in the same row indicate that scores are statistically different at $p \leq 0.05$ (based on one-way ANOVA and Tukey's post-hoc test).

	Test score (F)	Comparisons between stages		
		Growing (G)	Optimum (O)	Terminal (T)
NMDS1	8.2***	a	b	b
NMDS2	39.4***	a	b	c

*** $p \leq 0.001$.

the previous tree cohort, the regeneration processes of the stand had intensified; average tree height decreased and tree height variability increased. Decrease of the tree layer compactness significantly increased the inflow of light and water to the forest floor and accelerated the decomposition of accumulated organic matter (release of nutrients), which, a high level of disturbance, supported the clearings species (especially *Rubus hirtus*, *Senecio nemorensis and S. fuchsii*) and nitrophilous ruderal species (*Rumex obtusifolius*) and forest margins species (*Mycelis muralis*). It was also the cause of the high total cover and evenness of distribution of species in the herb layer. It also caused a decrease (compared to stage O) in the number of ancient forest species, beech forest species and alpha diversity.

The indicator species analysis shows changes in the C-S-R signature for herb vegetation of particular stages. We found a change from strategy R-C to C-R between G and O stages, followed by R-C-S strategies in T stage. Thus, as in the case of stages of forest succession, the life strategies implemented by herb layer vegetation varied at different stages of forest development (Chai et al., 2016). Stage O was characterised by the highest stability and abundance of habitats, hence it had the highest share of strategy C in the C-S-R signature. On the other hand, the increase in the share of stress-tolerance and the decrease in competitiveness in the T stage may be associated with a high degree of disturbances and stress related to the tree cutting and regeneration. It seems that the increase in the density and area of tree regenerations, which strongly compete with herb layer vegetation for resources, contributed to the increased importance of such species as Carex sylvatica, *Urtica dioica* and *Rubus hirtus*.

4.3. *Impact of developmental stages on dynamics of herb layer diversity and implications for future forest management strategies*

In the period 1970s – 2010s, managed under the shelterwood system, the forests of the Polish part of the Eastern Carpathians gradually aged (Durak and Holeksa, 2015; Bugno-Pogoda and Durak, 2021). In the 1970s, the stands in which the sample plots were located were the youngest and had the smallest volume. Hence, the stands of the plots from this period, best represented stage G (almost 1/3 of all plots). Moreover, at the same time, almost 2/3 of the plots were at stage O. During this period, the vegetation was severely disturbed because of the high forest management intensity (Kuemmerle et al., 2007, Bugno-Pogoda et al., 2021) and still practiced non-commercial forest use (especially cattle grazing, firewood collection and litter raking, Glatzel, 1991, Durak and Holeksa, 2015). Hence, the forests of the 1970s were characterised by indicator species with low light and trophic requirements (Bugno-Pogoda and Durak, 2021). The disturbances resulted in a large diversity of habitats, which overlapped with the previously discussed influence of competition from young stands. As a result, herb layer communities had a low evenness of distribution of species and a large number of species on the plots (Bugno-Pogoda et al., 2021).

In the 2000s, the average age of stands of the sampling plots exceeded 100 years and their stocking index and volume were the

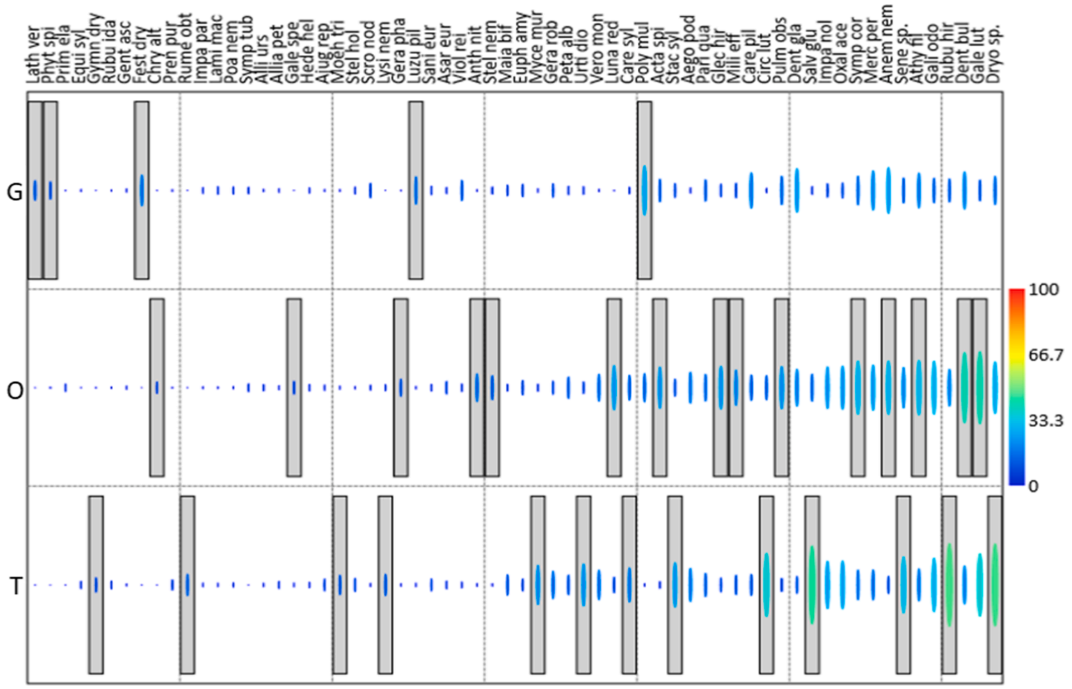

Fig. 5. Results of indicator species analysis. Values of indicator value of species (IndVal%) for forest developmental stages are presented. The statistical significances ($p < 0.05$) of the indicator values have been boxed.

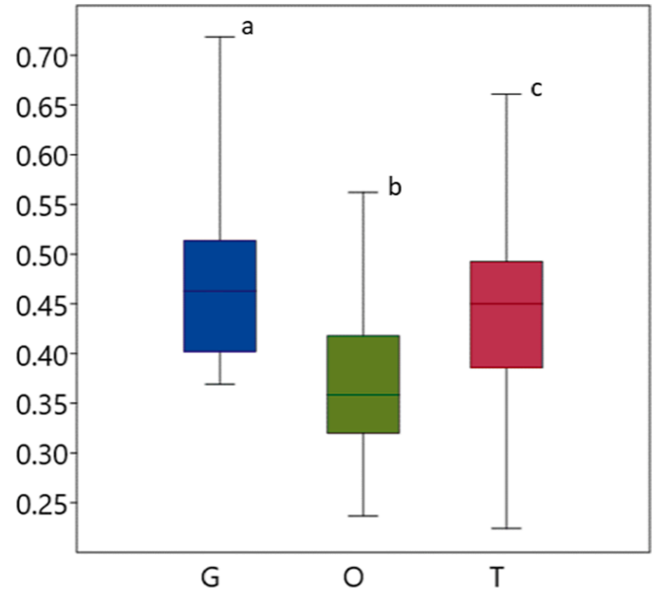

Fig. 6. Changes of the beta diversity (expressed by Simpson dissimilarity index) between developmental stages. For each stage, the 25–75 percent quartiles are drawn using a box. The median is shown with a horizontal line inside the box. The minimal and maximal values are shown with short horizontal lines ("whiskers"). Significance of differences was confirmed by one-way ANOVA ($F = 36.86$, $p < 0.001$); different letters indicate that scores are statistically different at $p \leq 0.05$ based on Tukey's post-hoc test.

largest. Compared to the 1970s, the pressure from forest treatments and non-commercial use decreased significantly, contributing to a decrease in spatial diversity of habitats and an increase in their stability (Durak and Holeksa, 2015). This was the effect of not only less severe forest management, but also a clear dominance of the O stage. Compared to the 1970s, the share of species associated with forest clearings increased, which seems to be related to the formation of gaps due to the silvicultural treatments in stands of the developmental stage O. In the 2000s, the greatest number of forest nitrophilic, shade-tolerant species (e.g. *Lysimachia nemorum*, *Paris quadrifolia*) and those that preferred the moisture soils (e.g. *Impatiens noli-tangere*, *Veronica montana* and *Stellaria nemorum*) were recorded in the herb layer. Compared to the 1970s beta diversity decreased, suggesting homogenisation of the species composition of herb layer vegetation (Bugno-Pogoda et al., 2021). In light of the results of the present work, it was the result of a decrease in disturbances and the dominance of the O stage, in which, as discussed previously, optimal habitat conditions are developed for typical forest species, an important metric of the conservation status of forests vegetation.

In the 2010s, the average age of stands exceeded 113 years, their stocking index and volume decreased compared to the previous research period; T stage dominated, when the felling of the old tree generation and development of a new tree generation intensified. Severe management treatment increased (Bugno-Pogoda et al., 2021). As a consequence, in the 2010s, the stands on the sampling plots had the lowest density and their average height was smaller and more variable than in the previous periods. The shrub layer had much more cover than in the past. As a result, compared to earlier periods, the alpha diversity and the number of species (including ancient forest species and beech forest species) that preferred, shaded habitats with moist, fertile soil with high pH (e.g. *Paris quadrifolia*, *Pulmonaria obscura*, *Anthriscus nitida*) decreased. The mechanism of changes in vegetation in this case is strongly related to changes in the structure of trees and shrubs, which was pointed out by other authors (e.g. Ujházy et al., 2005; Šamonil and Vrška, 2007).

The lowest beta and the highest alpha diversity was recorded in the 2000s (Bugno-Pogoda et al., 2021). Analysing the diversification of herb layer characteristics between the study periods, as well as between the stages, we found a great similarity between the 2000s and the O stage (e.g. in both cases the number of species, the number of species of ancient forests, L_L, N_H were the highest). Hence, it seems that the pattern of diversity in the 2000s was strongly influenced by the dominance of the O stage. It should be emphasised that the beta diversity, lower than in the 1970s, does not reduce the conservation value of the studied forests and was the result of a small spatial differentiation of stands (dominance of one stage) in the 2000s. In fact, forests from the 2000s have a high conservation value, as evidenced by a high number of species, including ancient, and beech forest species, as well as high alpha diversity (Bugno-Pogoda et al., 2021). The highest beta diversity was recorded in the 2010s, which was the result of a small similarity of the species composition (high species turnover) as well as the species richness between the plots (Bugno-Pogoda et al., 2021). In this case beta diversity was influenced by the high level of disturbances caused by the regeneration process of mature stands in aging forests, dominated by the T stage.

Our results indicate the significant role of the age and spatial structure of stands in controlling the species composition and diversity of herb layer vegetation in the forests of the Polish part of the Eastern Carpathians managed under the shelterwood systems. Hence, the significant implications for sustainable management of the herb layer, which should be included in future forest management strategies. Firstly, because the mosaic of different age-classes is of great importance for regional biodiversity (Schall et al., 2018), forest managers should ensure the creation and maintenance of stands with a more even share of basic development stages (stands with different ages). Secondly, the age differentiation of stands should be planned not only on a local scale (e.g. forest ranges or forest districts). Planning and supervision on a regional scale (e.g. the regional directorate of state forests or the Polish part of the Carpathians) is very important.

CRediT authorship contribution statement

Tomasz Durak: Conceptualization, Methodology, Investigation, Validation, Formal analysis, Data curation, Writing – original draft, Visualization, Writing – review & editing, Supervision, Funding acquisition. **Anna Bugno-Pogoda:** Conceptualization, Methodology, Investigation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Roma Durak:** Investigation, Formal analysis, Writing – review & editing, Visualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120233.

References

Anderson, M.J., 2001. A new method for non-parametric multivar iate analysis of variance. Aust. Ecol. 26 (1), 32–46.

Augusto, L., Ranger, J., Binkley, D., Rothe, A., 2002. Impact of several common tree species of European temperate forests on soil fertility. Ann. For. Sci. 59 (3), 233–253.

Banaś, J., Bujoczek, L., Zięba, S., Drozd, M., 2014. The effects of different types of management, functions, and characteristics of stands in Polish forests on the amount of coarse woody debris. Eur. J. Forest Res. 133, 1095–1107.

Barbier, S., Gosselin, F., Balandier, P., 2008. Influence of tree species on understory vegetation diversity and mechanisms involved – a critical review for temperate and boreal forests. For. Ecol. Manage. 254 (1), 1–15.

Baselga, A., 2010. Partitioning the turnover and nestedness components of beta diversity. Glob. Ecol. Biogeogr. 19, 134–143.

Braun-Blanquet, J. (Ed.), 1964. Pflanzensoziologie. Springer Vienna, Vienna.

Bugno-Pogoda, A., Durak, R., Durak, T., 2021. Impact of forest management on the temporal dynamics of herbaceous plant diversity in the Carpathian beech forests over 40 years. Biology. 10, 406.

Bugno-Pogoda, A., Durak, T., 2021. Climate and management factors underlying changes in beech forest herbaceous layer plant communities in the polish eastern Carpathians. Forests. 12, 1446.

Bürgi, M., Gimmi, U., Stuber, M., 2013. Assessing traditional knowledge on forest uses to understand forest ecosystem dynamics. For. Ecol. Manage. 289, 115–122.

Caccianiga, M., Luzzaro, A., Pierce, S., Ceriani, R.M., Cerabolini, B., 2006. The functional basis of a primary succession resolved by CSR classification. Oikos 112, 10–20.

Chai, Y., Yue, M., Wang, M., Xu, J., Liu, X., Zhang, R., Wan, P., 2016. Plant functional traits suggest a change in novel ecological strategies for dominant species in the stages of forest succession. Oecologia 180 (3), 771–783.

Cole, D.W., Rapp, M., 1981. Elemental cycling in forest ecosystems. In: Reichle, D.E. (Ed.), Dynamic properties of forest ecosystems. Cambridge University Press, Cambridge, UK, pp. 341–409.

Coomes, D.A., Grubb, P.J., 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecol. Monogr. 70 (2), 171–207.

De Lombaerde, E., Verheyen, K., Perring, M.P., Bernhardt-Römermann, M., Van Calster, H., Brunet, J., Chudomelová, M., Decocq, G., Diekmann, M., Durak, T., Hédl, R., Heinken, T., Hommel, P., Jaroszweicz, B., Kopecký, M., Lenoir, J., Macek, M., Máliš, F., Mitchell, F.J.G., Naff, T., Newman, M., Petřík, P., Reczyńska, K., Schmidt, W., Świerkosz, K., Vild, O., Wulf, M., Baeten, L., 2018. Responses of competitive understorey species to spatial environmental gradients inaccurately explain temporal changes. Basic Appl. Ecol. 30, 52–64.

DeYoung, J., 2016. Forest Measurements: An Applied Approach –. Open Oregon Educational Resources.

Dufrêne, M., Legendre, P., 1997. Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecol. Monogr. 67 (3), 345–366.

Durak, T., Durak, R., Węgrzyn, E., Leniowski, K., 2015. The impact of changes in species richness and species replacement on patterns of taxonomic homogenization in the Carpathian forest ecosystems. Forests. 6, 4391–4402.

Durak, T., Holeksa, J., 2015. Biotic homogenisation and differentiation along a habitat gradient resulting from the ageing of managed beech stands. For. Ecol. Manag. 351, 47–56.

Durak, T., Durak, R., 2016. How biotic differentiation of human impacted nutrient poor deciduous forests can affect the preservation status of mountain forest vegetation. Forests. 7, 241.

Durak, T., Bugno-Pogoda, A., Durak, R., 2021. Application of forest inventories to assess the forest developmental stages on plots dedicated to long-term vegetation studies. For. Ecol. Manage. 489, 119041.

Dzwonko, Z., 1977. Forest communities of the Gory Słonne Range (Polish Eastern Carpathians). Fragm. Flor. Geobot. 23, 161–200.

Dzwonko, Z., Loster, S., 2001. Wskaźnikowe gatunki roślin starych lasów i ich znaczenie dla ochrony przyrody i kartografii roślinności. IGiPZ PAN. Pr. Geogr. 178, 120–132.

Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W., Paulissen, D., 1992. Zeigerwerte von pflanzen in Mitteleuropa. Scr. Geobot. 18, 1–248.

Gilliam, F.S., Turrill, N.L., Adams, M.B., 1995. Herbaceous-layer and overstory species in clear-cut and mature central Appalachian hardwood forest. Ecol. Appl. 5, 947–955.

Gilliam, F.S., Roberts, M.R., 2003. Interactions between the herbaceous layer and overstory canopy of eastern forests: a mechanism for linkage. In: Gilliam, F.S., Roberts, M.R. (Eds.), The Herbaceous Layer in Forests of Eastern North America. Oxford University Press, New York.

Gilliam, F.S., 2007. The ecological significance of the herbaceous layer in temperate forest ecosystems. Bioscience 57, 845–858.

Glatzel, G., 1991. The impact of historic land use and modern forestry on nutrient relations of Central European forest ecosystems. Fertil. Res. 27, 1–8.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169–1194.

Grime, J.P., 2001. Plant Strategies, Vegetation Processes and Ecosystem Properties, 2nd ed. Wiley, Chichester.

Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: paleontological statistics software package for education and data analysis. Palaeontol. Electronica 4, 1–9.

Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biol. Conserv. 91, 9–22.

Hessburg, P.F., Miller, C.L., Parks, S.A., Povak, N.A., Taylor, A.H., Higuera, P.E., Prichard, S.J., North, M.P., Collins, B.M., Hurteau, M.D., Larson, A.J., Allen, C.D., Stephens, S.L., Rivera-Huerta, H., Stevens-Rumann, C.S., Daniels, L.D., Gedalof, Z., Gray, R.W., Kane, V.R., Churchill, D.J., Hagmann, R.K., Spies, T.A., Cansler, C.A., Belote, R.T., Veblen, T.T., Battaglia, M.A., Hoffman, C., Skinner, C.N., Safford, H.D., Salter, R.B., 2019. Climate, environment, and disturbance history govern resilience of western North American forests. Front. Ecol. Evol. 7, 239.

Hunt, R., Hodgson, J.G., Thompson, K., Bungener, P., Dunnett, N.P., Askew, A.P., 2004. A new practical tool for deriving a functional signature for herbaceous vegetation. Appl. Veg. Sci. 7, 163–170.

Jaworski, A., Kołodziej, Z., Porada, K., 2002. Structure and dynamics of stands of primeval character in selected areas of the Bieszczady National Park. J. For. Sci. 48, 185–201.

Korpel, S., 1995. Die Urwalder der Westkarpaten. Gustav Fischer Verlag, Stuttgart.

Krishna, M.P., Mohan, M., 2017. Litter decomposition in forest ecosystems: a review. Energy Ecol. Environ. 2, 236–249.

Kuemmerle, T., Hostert, P., Radeloff, V.C., Perzanowski, K., Kruhlov, I., 2007. Postsocialist forest disturbance in the Carpathian border region of Poland, Slovakia, and Ukraine. Ecol. Appl. 17, 1279–1295.

Landuyt, D., De Lombaerde, E., Perring, M., Hertzog, L., 2019. The functional role of temperate forest understorey vegetation in a changing world. Glob. Chang. Biol. 25 (11), 3625–3641.

Matuszkiewicz, W., 2001. Przewodnik do Oznaczania Zbiorowisk Roślinnych Polski [A Guide for the Identification of Polish Plant Communities]. Wydawnictwo Naukowe PWN, Warsaw.

McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark, J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J., Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte, M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. Science 368, eaaz9463.

Meteorological Data. Averages and Monthly Totals. Lesko. Available online: https://meteomodel.pl (accessed on 16 March 2021).

Meyer, P., 1999. Bestimmung der Waldentwicklungsphasen und der Texturdiversitat in Naturwaldern. Allg. F. u. J. Ztg. 170, 203–211.

Milad, M., Schaich, H., Bürgi, M., Konold, W., 2011. Climate change and nature conservation in Central European forests: a review of consequences, concepts and challenges. Forest Ecol. Manage. 261, 829–843.

Mirek, Z., Piękoś-Mirkowa, H., Zając, M., Zając, A, 2002. Flowering plants and pteridophytes of Poland of Poland – a checklist. In: Mirek, Z. (Ed.), Biodiversity of Poland 1. W. Szafer Institute of Botany, Polish Academy of Sciences, Krakow.

Olden, J.D., Poff, N.L., 2003. Toward a mechanistic understanding and prediction of biotic homogenization. Am. Nat. 162, 442–460.

Perring, M.P., Bernhardt-Römermann, M., Baeten, L., Midolo, G., Blondeel, H., Depauw, L., Landuyt, D., Maes, S.L., De Lombaerde, E., Carón, M.M., Vellend, M., Brunet, J., Chudomelová, M., Decocq, G., Diekmann, M., Dirnböck, T., Dörfler, I., Durak, T., De Frenne, P., Gilliam, F.S., Hédl, R., Heinken, T., Hommel, P., Jaroszewicz, B., Kirby, K.J., Kopecký, M., Lenoir, J., Li, D., Máliš, F., Mitchell, F.J.G., Naaf, T., Newman, M., Petřík, P., Reczyńska, K., Schmidt, W., Standovár, T., Świerkosz, K., Van Calster, H., Vild, O., Wagner, E.R., Wulf, M., Verheyen, K., 2018. Global environmental change effects on plant community composition trajectories depend upon management legacies. Glob. Chang. Biol. 24, 1722–1740.

Pierce, S., Brusa, G., Vagge, I., Cerabolini, B.E.L., Thompson, K., 2013. Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. Funct. Ecol. 27 (4), 1002–1010.

Pierce, S., Negreiros, D., Cerabolini, B.E.L., Kattge, J., Díaz, S., Kleyer, M., Shipley, B., Wright, S.J., Soudzilovskaia, N.A., Onipchenko, V.G., van Bodegom, P.M., Frenette-Dussault, C., Weiher, E., Pinho, B.X., Cornelissen, J.H.C., Grime, J.P., Thompson, K., Hunt, R., Wilson, P.J., Buffa, G., Nyakunga, O.C., Reich, P.B., Caccianiga, M., Mangili, F., Ceriani, R.M., Luzzaro, A., Brusa, G., Siefert, A., Barbosa, N.P.U., Chapin, F.S., Cornwell, W.K., Fang, J., Fernandes, G.W., Garnier, E., Le Stradic, S., Peñuelas, J., Melo, F.P.L., Slaviero, A., Tabarelli, M., Tampucci, D., 2017. A global method for calculating plant CSR ecological strategies applied across biomes world-wide. Funct. Ecol. 31, 444–457.

Rackham, O., 2008. Ancient woodlands: Modern threats. New Phytol. 180, 571–586.

Rooney, T.P., Wiegmann, S.M., Rogers, D.A., Waller, D.M., 2004. Biotic impoverishment and homogenization in unfragmented forest understory communities. Conserv. Biol. 18, 787–798.

Rooney, T.P., 2009. High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. Plant Ecol. 202, 103–111.

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., Mori, A., 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 (1), 267–278.

Schmitz, A., Sanders, T.G.M., Bolte, A., Bussotti, F., Dirnböck, T., Johnson, J., Peñuelas, J., Pollastrini, M., Prescher, A.-K., Sardans, J., Verstraeten, A., de Vries, W., 2019. Responses of forest ecosystems in Europe to decreasing nitrogen deposition. Environ. Pollut. 244, 980–994.

Simpson, G.G., 1943. Mammals and the nature of continents. Am. J. Sci. 241, 1–31.

Skiba, S., Drewnik, M., 2003. Soil map of the polish carpathian mountains. Rocz. Bieszcz. 11, 15–20.

Standovár, T., Kenderes, K., 2003. A review on natural stand dynamics in Beechwods of East Central Europe. Appl. Ecol. Environ. Res. 1, 19–46.

Steubing, L., Fangmeier, A., Both, R., Frankenfeld, M., 1989. Effects of SO2, NO2, and O3 on population development and morphological and physiological parameters of native herb layer species in a beech forest. Environ. Pollut. 58 (4), 281–302.

Šamonil, P., Vrška, T., 2007. Trends and cyclical changes in natura l fir-beech Forests at the north-western edge of the Carpathians. Folia Geobotanica. 42 (4), 337–361.

Trap, J., Bureau, F., Brethes, A., Jabiol, B., Ponge, J.-F., Chauvat, M., Decaëns, T., Aubert, M., 2011. Does moder development along a pure beech (Fagus sylvatica L.) chronosequence result from changes in litter production or in decomposition rates? Soil Biol. Biochem. 43 (7), 1490–1497.

Ujházy, K., Križová, E., Vančo, M., Freňáková, E., Ondruš, M., 2005. Herb layer dynamics of primeval fir-beech forests in central Slovakia. In: Commarmot, B.; Hamor, F. D. (eds): Natura l Forests in the Temperate Zone of Europe - Values and Utilisation. Conference 13-17 October 2003, Mukachevo, Ukraine. Proceedings. Birmensdorf, Swiss Federal Research Institute WSL; Rakhiv, Carpathian Biosphere Reserve. 193-202.

Ujházy, K., Hederová, L., Máliš, F., Ujházyová, M., Bosela, M., Čiliak, M., 2017. Overstorey dynamics controls plant diversity in age-class temperate forests. For. Ecol. Manage. 391, 96–105.

Vacek, S., Černý, T., Vacek, Z., Podrázský, V., Mikeska, M., Králíček, I., 2017. Long-term changes in vegetation annd site conditions in beech and spruce forest of lower mountains ranges of Central Europe. For. Ecol. Manage. 398, 75–90.

Van Calster, H., Baeten, L., De Schrijver, A.n., De Keersmaeker, L., Rogister, J.E., Verheyen, K., Hermy, M., 2007. Management driven changes (1967–2005) in soil acidity and the understorey plant community following conversion of a coppice-with-standards forest. For. Ecol. Manage. 241 (1-3), 258–271.

Verheyen, K., Honnay, O., Motzkin, G., Hermy, M., Foster, D.R., 2003. Response of forest plant species to land-use change: a life-history trait-based approach. J. Ecol. 91 (4), 563–577.

Xanthopoulos, P., Pardalos, P.M., Trafalis, T.B. 2013. Linear Discriminant Analysis. In: Robust Data Mining. SpringerBriefs in Optimization. Springer, New York, NY.

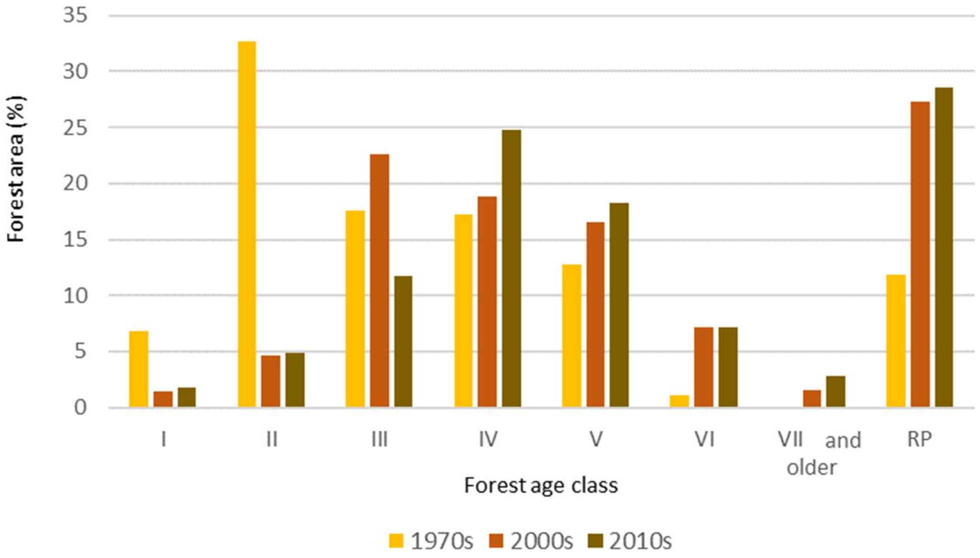

Fig. A1. Proportion of the forest area by age class in the Sanocko-Turczańskie Mountains in the 1970s, 2000s and 2010s. RP - stands in the regeneration period.

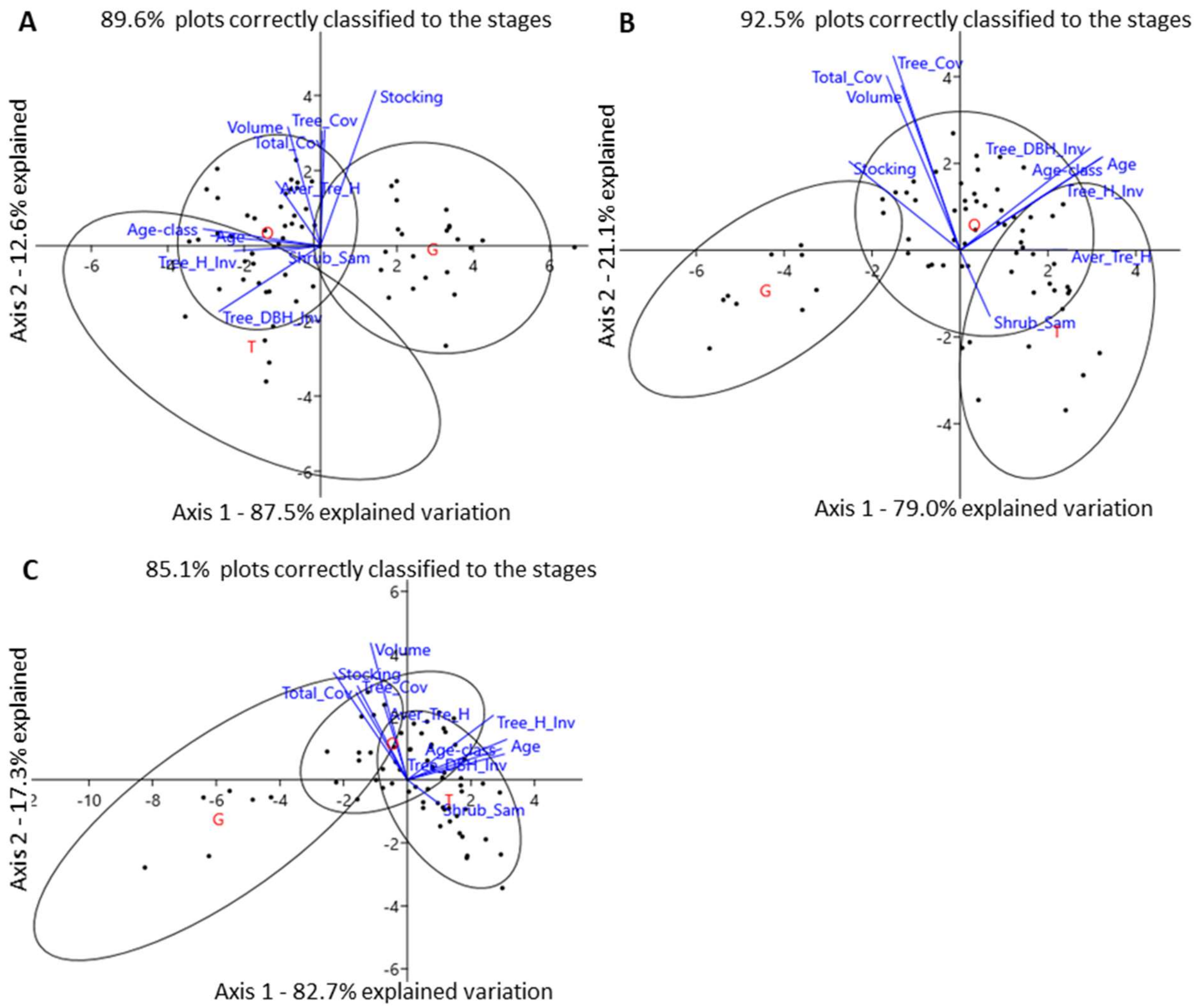

Fig. A2. Comparison of stand variables composition of forest stages determined by the LDA analysis based on data for the 1970s (A), 2000s (B) and 2010s (C). The groups are marked with 95% ellipses. Variable abbreviations are explained in Table A1.

Table A1. Correlation between stand variables and NMDS axes that represent changes in herb species composition from Growing to Terminal stage ("+" and "−" symbols denote positive or negative trend, respectively; Spearman rank correlation test). ** $p \leq 0.01$, *** $p \leq 0.001$.

Abbreviation	Unit	Description	Spearman's correlation	
			NMDS 1	NMDS 2
Stocking	-	Measure which is determined by the ratio of estimated growing stock of a stand per 1 ha (merchantable volume) to merchantable growing stock given in yield tables (for the same tree species, the same site class and the same age).	ns	− ***
Tree_DBH_Inv	cm	Mean DBH specified for dominant species, on the basis of random measurements of 5-10 trees made in places representative for a given sub-compartment.	+ **	+ ***
Tree_H_Inv	m	Mean height specified for dominant species, on the basis of random measurements of 5-10 trees made in places representative for a given sub-compartment.	ns	+ ***
Volume	m^3/1 ha	Estimated total volume of trees with breast height diameter from 7 cm up (recorded in a stand description referred to 1 ha).	ns	ns
Age-class	age-classes separated by 20-year interval	Ascription of age-class based on age of dominant species.	+ **	+ ***
Age	years	Mean age for dominant species.	+ ***	+ ***
Total_Cov	%	Total cover of tree and shrub layer.	ns	− **
Tree_Cov	%	Cover of tree layer.	ns	− ***
Shrub_Sam	%	Cover of shrub layer.	ns	+ ***
Aver_Tre_H	m	Average height of trees.	ns	ns

Tab.A2. Comparison of development stages in old-growth and managed Carpathian beech forests.

	Stages sensu Korpel 1995			Broadly defined stages in managed Carpathian beech forests (distinguished based on the method of Durak et al. 2021)		
Development stage type	Growing-up	Optimum	Breakdown	Growing	Optimum	Terminal
Characteristic processes / forest management treatments	Ongoing growth; steadily increasing biomass	Biomass culmination	Decrease in biomass; thick trees belonging to the older generation begin dying and increase the volume of deadwood	Forest stands during maintenance cuts (thinning); increasing biomass	Pre-felling stands (advance thinning), maximum biomas	Felling stands in regeneration period (regular / irregular shelterwood); low biomas
Age (years)	40-90 1)	90-130 1)	130-220 1)	62-65	96-113	97-121
Volume (m^3/ha)	423-717 2)	536-759 2)	559-687 2)	243-429	303-449	196-287
Mean height (m)	24 2)	31 2)	27 2)	21-25	26-31	27-32
Mean DBH (cm)	33 2)	47 2)	40 2)	26-30	42-52	53-57
Stocking	high 1)	medium 1)	low 1)	0.7-1.1	0.6-0.8	0.3-0.5

1) based on Standovár and Kenderes (2003)

2) based on Jaworski et al. (2002)

Table A3. Indicator species for forest developmental stages. L, T, F, R, N: Ellenberg's indicator values for light, temperature, moisture, reaction and nitrogen, respectively (according to Ellenberg et al., 1992). C-S-R life strategies were adopted following Pierce et al. (2017).

Stage	Ellenberg indicator values					Life strategy			
	L	T	F	R	N	C (%)	S (%)	R (%)	CSR
Growing (G)									
Phyteuma spicatum	x	x	5	6	5	50	0	50	CR
Festuca drymeia	-	-	-	-	-	-	-	-	-
Lathyrus vernus	4	6	5	8	4	40	0	60	CR
Luzula pilosa	2	x	5	5	4	28	19	54	R/CSR
Polygonatum multiflorum	2	x	5	6	5	42	0	58	CR
Mean values	*2.7*	*6.0*	*5.0*	*6.3*	*4.5*	*40*	*5*	*55*	
Optimum (O)									
Dentaria bulbifera	3	5	5	7	6	24	0	76	R/CR
Lunaria rediviva	4	5	6	7	8	61	0	39	CR
Chrysosplenium alternifolium	4	4	8	7	5	22	0	78	R/CR
Galeopsis speciosa	7	x	5	x	8	-	-	-	
Geranium phaeum	6	x	5	6	5	64	0	36	C/CR
Anthriscus nitida	4	4	6	8	8	59	17	24	C/CSR
Stellaria nemorum	4	x	7	5	7	27	4	69	R/CR
Actaea spicata	3	5	5	6	7	61	15	24	C/CSR
Glechoma hirsuta	-	-	-	-	-	-	-	-	-
Milium effusum	4		5	5	5	34	16	50	CR/CSR
Pulmonaria obscura	4	5	6	8	7	58	0	42	CR
Symphytum cordatum	-	-	-	-	-	-	-	-	-
Anemone nemorosa	x	x	5	x	x	38	11	51	CR
Athyrium filix-femina	3	x	7	x	6	69	0	31	C/CR
Galeobdolon luteum	3	5	5	7	5	29	37	34	CSR
Mean values	*4.1*	*4.7*	*5.8*	*6.6*	*6.4*	*45*	*8*	*46*	
Terminal (T)									
Salvia glutinosa	4	5	6	7	7	58	0	42	CR
Rubus hirtus	7	4	5	x	x	22	65	13	S/CS
Dryopteris sp.	-	-	-	-	-	-	-	-	-
Circaea lutetiana	4	5	6	7	7	43	0	57	CR
Gymnocarpium dryopteris	3	4	6	4	5	33	10	56	R/CSR
Rumex obtusifolius	7	5	6	x	9	-	-	-	-
Moehringia trinervia	4	5	5	6	7	11	0	89	R
Lysimachia nemorum	2	5	7	7	7	-	-	-	-
Mycelis muralis	4	6	5	x	6	29	11	60	R/CSR
Urtica dioica	x	x	6	7	8	45	34	21	CS/CSR
Stachys sylvatica	4		7	7	7	44	0	56	CR
Senecio sp.	7	-	-	-	8	-	-	-	-
Carex sylvatica	2	5	5	6	5	29	40	30	CR/CSR
Mean values	*4.4*	*4.9*	*5.8*	*6.4*	*6.9*	*35*	*18*	*47*	

Table A4. Frequencies (%) for herb layer species in forest developmental stages in 1970s, 2000s and 2010s. Only species that occurred in dataset from 1970s to 2010s at least 10 times (i.e. with 5% frequency) are included.

	1970s			2000s			2010s		
	G	O	T	G	O	T	G	O	T
Lathyrus vernus	18	3	0	11	4	0	17	0	3
Phyteuma spicatum	18	8	0	11	4	0	0	0	0
Primula elatior	5	13	0	0	6	9	0	0	0
Equisetum sylvaticum	9	5	0	0	4	0	0	0	11
Populus tremula	18	5	40	0	2	0	0	0	3
Gymnocarpium dryopteris	5	3	20	0	9	9	0	0	11
Rubus idaeus	0	5	0	22	9	36	0	0	0
Gentiana asclepiadea	5	15	20	0	2	0	17	0	6
Festuca drymeia	9	5	20	22	2	0	50	0	6
Chrysosplenium alternifolium	5	25	20	0	2	0	0	0	0
Prenanthes purpurea	9	5	40	0	4	36	0	4	0
Rumex obtusifolius	0	0	0	0	4	9	17	8	19
Euonymus europaea	9	5	0	11	17	0	0	0	0
Impatiens parviflora	0	0	0	44	9	9	0	12	6
Lamium maculatum	0	5	0	33	4	9	17	8	8
Poa nemoralis	14	0	20	11	11	18	0	8	3
Symphytum tuberosum	14	13	0	11	11	9	0	4	0
Allium ursinum	9	8	20	0	11	9	0	12	6
Sorbus aucuparia	14	13	0	11	13	0	0	8	0
Alliaria petiolata	9	13	0	0	11	9	17	4	11
Galeopsis speciosa	0	8	40	11	26	18	0	0	0
Lonicera xylosteum	23	25	20	0	6	9	0	0	0
Sambucus racemosa	9	13	20	33	13	9	0	0	6
Hedera helix	9	10	0	11	15	0	17	8	14
Ajuga reptans	14	10	20	0	17	18	0	4	11
Moehringia trinervia	9	5	40	0	9	36	17	16	11
Stellaria holostea	9	8	0	22	13	9	17	4	19
Carpinus betulus	9	10	20	11	15	27	17	0	11
Scrophularia nodosa	18	15	20	22	15	9	17	0	6
Lysimachia nemorum	0	0	0	11	26	45	0	8	14
Geranium phaeum	9	35	0	0	15	9	0	0	6
Luzula pilosa	18	8	20	33	17	9	33	8	11
Sanicula europaea	27	23	80	0	13	9	0	4	11
Asarum europaeum	18	18	0	11	19	9	17	16	17
Viola reichenbachiana	32	13	20	11	28	18	33	0	11
Acer platanoides	0	3	0	44	43	36	33	0	14
Anthriscus nitida	14	28	20	0	40	18	0	0	3
Daphne mezereum	41	43	80	11	11	9	0	4	3
Stellaria nemorum	14	20	40	22	47	27	0	0	0
Maianthemum bifolium	18	15	20	33	26	36	17	8	22
Corylus avellana	18	43	60	0	23	18	17	12	11
Euphorbia amygdaloides	36	23	20	11	30	27	0	16	17
Mycelis muralis	14	18	60	11	26	45	17	16	31
Ulmus glabra	14	33	0	11	45	18	0	20	6

Ribes uva-crispa	41	43	20	11	28	27	17	4	8
Geranium robertianum	41	55	80	11	21	18	17	8	31
Petasites albus	36	50	60	0	32	36	0	28	19
Urtica dioica	23	45	0	33	28	45	17	20	44
Veronica montana	9	30	40	33	62	64	0	12	25
Lunaria rediviva	9	43	0	0	51	27	0	48	31
Fraxinus excelsior	23	48	40	44	64	64	17	20	3
Carex sylvatica	18	30	40	44	51	55	17	36	36
Polygonatum multiflorum	64	58	0	67	43	36	17	20	8
Actaea spicata	59	63	60	22	49	27	0	32	11
Stachys sylvatica	36	38	60	56	45	55	17	28	44
Aegopodium podagraria	18	58	0	33	47	36	33	32	44
Paris quadrifolia	36	48	60	67	57	45	17	16	33
Glechoma hirsuta	41	58	60	22	66	36	0	28	19
Milium effusum	32	53	60	33	55	27	33	44	31
Carex pilosa	55	48	100	33	51	45	50	48	33
Circaea lutetiana	23	55	80	33	57	73	17	24	53
Pulmonaria obscura	68	78	60	44	60	64	0	20	14
Dentaria glandulosa	55	70	20	56	51	18	67	68	56
Sambucus nigra	50	70	40	78	60	36	33	64	47
Salvia glutinosa	36	63	100	22	57	64	50	60	72
Impatiens noli-tangere	36	68	80	56	68	55	50	68	56
Oxalis acetosella	59	65	100	56	77	82	17	36	50
Fagus sylvatica	59	60	60	100	89	100	67	56	22
Abies alba	77	65	100	44	70	91	33	52	53
Symphytum cordatum	59	75	60	56	74	55	50	64	58
Mercurialis perennis	68	75	100	56	74	73	67	60	47
Anemone nemorosa	59	53	20	78	91	82	67	76	47
Senecio sp.	64	65	80	67	77	73	33	68	72
Athyrium filix-femina	91	88	100	100	98	100	0	16	33
Galium odoratum	68	83	100	78	77	73	50	92	67
Rubus hirtus	64	65	100	89	77	82	83	80	89
Acer pseudoplatanus	77	65	100	67	89	100	83	84	64
Dentaria bulbifera	77	100	80	78	94	91	67	88	67
Galeobdolon luteum	77	100	100	89	100	82	50	92	83
Dryopteris sp.	86	85	100	67	98	100	100	100	92