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Examination of Forest Steppe Species in the Case of Areas Where Traditional Cultivation Was Abandoned

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Abstract: The thousands of kilometers of forest steppes in Eurasia belong to the most threatened ecosystems thanks to habitat loss. We have limited knowledge on the recolonization ability of forest steppe species to date, which is the reason we examined the textural and structural changes in these species during secondary succession in areas of different former land use. The species number, cover, and diversity of forest steppe species, especially those of the *Festuco-Brometea* group, became significant for all three types in the oldest fallows. The number and proportion of forest steppe species have been steadily increasing in abandoned vineyards and arable land, indicating that forest steppe species are able to rapidly recolonize. The increase in the number and cover of forest steppe species in abandoned grasslands reveals that the replacement of the species pool of these grasslands is not necessarily accompanied by degradation, but also by the appearance and spread of valuable natural species if the habitat is sufficiently patchy. The proportions of habitat categories level off in abandoned vineyards and arable land as abandonment progresses. The cover rates of disturbed habitats species were negligible for all three types for the third decade after abandonment, indicating a change in the quality of the species pool.

Keywords: age groups; space for time; vineyards; arable; grasslands; species richness; cover; diversity; habitat categories; coenosystematical groups; forest steppe patches

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1. Introduction

Palearctic forest steppe vegetation is a type of transitional vegetation between closed forests and steppe zones, formed by a mosaic of mainly closed forests and closed grasslands. Due to its complexity, this vegetation provides an important habitat for many endangered species and represents an important biodiversity hotspot [1]. Forest steppes belong to the most threatened ecosystems due to habitat loss and insufficient protection [2–4]. The wooded steppes of the Carpathian Basin form the western edge of the Eurasian-forest steppe zone [5–7]. This extensive grassland stretches over 8000 km from the Pannonian lowland to China [5,8] and is a characteristic zonal vegetation belt in Hungary [9]. Forest steppe (FS) forests were once typical habitat types in the plains and hills of the Carpathian Basin [6]. Hungarian FS can be divided into two major types: continental and sub-Mediterranean. The former type appears, for example, at the foothills and in the valleys of the North Hungarian Mountains, while the latter is more common in the southern part of the Plain [9].

The formation of the forest steppe forests in the Carpathian Basin can be explained by the characteristic transient climatic conditions there, in addition to the history of the vegetation, and phytogeographical and pedological conditions [6,10,11]. Historical and uses also played a major role in shaping the appearance of the forest steppe zone [6,12,13].

After centuries of decline, due to the pressures caused by human impact (e.g., agriculture and intensive land use), this diverse vegetation type can only be found in fragments in the Carpathian Basin, which is the reason that it has become rare and endangered [12,14]. The fragments remaining in their natural state are also of high importance in nature conservation at the international level [6].

Their international significance is shown by the fact that the forest and shrub components of the forest steppe patches are among the most important habitats that are protected or endangered in the European Union Habitats Directive, such as the marked habitats with the codes 40A0, 6210, 91H0, 91I0 and 91N0 [15]. Semi-dry grasslands of central Europe are recognized by the European Community as an endangered habitat, and 'Sub-Pannonic steppic grasslands' (6240), and also as a Natural Habitat Type of Community Interest, according to Annex I of the Habitats Directive (92/43/EEC) [16]. The *Bromus erectus*- and *Brachypodium pinnatum*-dominated semi-dry grasslands (6210) are regarded as highly valuable remnants of the original Pannonian forest steppe vegetation [10,16–23] and are also a NATURA 2000 habitat type [24,25].

The semi-arid grasslands and forest steppe meadows (*Brachypodium* grasslands) characterized by *Brachypodium* and *Bromus* species are common habitats in deciduous forests throughout Europe and in the forest steppe zones in Central and Eastern Europe [24,26]. In the European phytosociological school, semi-dry grasslands are classified in the class of *Festuco-Brometea,* Br.-Bl. and Tüxen ex Soó, 1947. Most European calcifrequent semi-dry grasslands are assigned into two alliances: the grasslands of *Cirsio-Brachypodion pinnati,* Hadač and Klika ex Klika, 1951, contain several continental species and develop on deeper, calcareous soils in the warm and dry areas of central Europe, while the grasslands of *Bromion erecti,* Koch, 1926, are distributed in the cooler regions, which mainly contain oceanic species [16].

The grasslands dominated by *Brachypodium pinnatum* developed from their edges or thickets in the vicinity of light-rich, open, dry–semi-arid (xerophilic, xero-mesophilic) forests. They typically create a mosaic effect with sloping steppes, shrub clusters, pubescent oaks and relic oak forests. To a significant extent, two groups of species are responsible for the diversity of the grassland species' composition: one is related to the former forest (*Quercetalia pubescentis-petraeae*) and the other group belongs to open associations and dry grassland (*Festuco-Brometea*, *Festucetalia valesiacae*) species [26]. *Brachypodium* grasslands are secondary developments and can be found at deforestation sites, abandoned areas of former extensive vineyards and orchards. Their stands are maintained by grazing and mowing [24,27,28]. These grasslands are one of the most species-rich habitats in the Carpathian Basin, with their natural stands containing up to 40–50 species within a few square meters. Importantly, they are capable of preserving the forest-edge flora and forest flora for centuries, even in a completely forest-free landscape [26–29].

Under semi-natural, undisturbed conditions, these species-rich grasslands have been shown to change slowly, partly towards afforestation, shrub encroachment and steppe expansion. However, due to the ongoing dry conditions at the site, the species pool in the stands is changing rapidly: forest species are disappearing, and steppe and dry grassland species are proliferating. The dominant *Brachypodium* is being replaced by other species, which, in turn, leads to the extinction of the forest steppe [26].

About two-thirds of the grasslands dominated by *Brachypodium pinnatum* in the Carpathian Basin are located in the North Hungarian Mountains [24,26]. Hungary also has the highest number of abandoned areas in the North Hungarian Mountains [30,31]. Abandoned lands are excellent objects for secondary succession studies [32–34]. In the northern foothills of the Bükk Mountains, the previously extensively cultivated abandoned areas in the Tardonai Hills demonstrated good regenerative potential. This is mainly due to the patchy nature of the landscape and the many smaller, semi-natural, refuge vegetation patches. Several forest steppe species can be found in these regenerating abandoned lands [31].

Due to their intricacy, forest steppe complexes, in their natural state, are often outstandingly rich in species in relation to their environment. In addition to forest and steppe-dwelling plants and animal species, they also contain so-called forest steppe species associated with forest edges and semi-shaded micro-habitats, which are protected from extremes [15]. In recent decades, several researchers have addressed these issues [35–37]. The range of forest steppe species was most comprehensively defined in the synthesis of 35Kun and Bölöni [15].

Within the framework of this study, we examined the secondary succession of forest steppe species in abandoned areas with different land-use histories (vineyards, arable land, hayfields/pastures), looking at four different age groups for the same landscape, using the 'space for time' method [33]. We were looking for answers regarding how forest steppe species can successfully colonize previously extensively cultivated abandoned areas during secondary succession.

The following questions were addressed:

(1) How does the total species richness, relative cover and diversity of forest steppe species of abandoned land vary by former cultivation type and age group?
(2) How did the relative species number and cover of habitat categories in cultivation types change after abandonment?
(3) What were the typical coenogroups in the case of forest steppe species and in the studied types and age groups, and how did their proportion change after abandonment?

2. Materials and Methods

2.1. Study Site

The location of the research was an approximately 4 km^2 area of the Tardonai Hills in the northeastern part of the Bükk Mountains, situated in north-eastern Hungary; see [31]. The studied area belongs to Sajókápolna [14]. Since the 1980s, more and more plots have been abandoned in the selected area, as was typical in other microregions in the North Hungarian Mountains [30]. The average temperature in the area is 9 °C, and the average annual rainfall is 600 mm [38]. The elevated plots ranged in height from 180 m to 280 m and varied in size from 0.15 ha to 1 ha [31]. Brown forest soils were predominantly formed on clay sediments, Pannonian sand, and their crumbs were mainly mixed with rhyolite tuff [39].

The vegetation of the research area is patchy in nature. The semi-natural vegetation consists of smaller forest and shrub patches and varying extents of regenerating grasslands. Most of the semi-natural forest patches can be classified into *Circaeo-Carpinetum* (Soó and Pócs 1957 em. Salt 1980), *Carici pilosae-Carpinetum* (Neuhausl and Neuhauslová-Novotná 1964 em. Borhidi 1996), *Quercetum petraeae-cerris* (Soó 1963) and *Corno-Quercetum pubescentis* (Jakucs and Zólyomi ex Máthé et Kovács 1962 associations). The expansion of scrub patches is locally significant; the main types are dominated by *Prunus spinosa*, *Crataegus* spp. and *Rosa* spp. The semi-natural grass patches are mainly classified as *Festuco-Brometea* (and, within that, mainly *Festucetalia valesiacae,* e.g., *Pulsatillo montanae-Festucetum rupicolae* (Dostál 1933/Soó 1964 corr. Borhidi 1997) and *Brometalia erecti* orders e.g., *Cirsio pannonici-Brachypodion pinnati* (Hadac and Klika 1944 associations)). The proportion of forest plantations formed by alien tree species (Robinia forest) is relatively low [40].

2.2. Botanical Sampling

In the framework of secondary succession studies, botanical samplings were carried out on abandoned plots of different cultivation types, such as vineyards, arable lands, pastures and hayfields (the latter two are collectively called grassland types, due to their similar nature). From the date of abandonment, the plots were divided into the following four age groups: age group 1 (abandoned 1–5 years), age group 2 (abandoned 6–10 years), age group 3 (abandoned 11–20 years) and age group 4 (abandoned 21–30 years ago). In this way, so-called chronological sequences were created, which formed the basis of the space-for-time substitution study. A minimum of 3–3 parcels were botanically recorded for each abandonment type and age group. During the botanical surveys in each parcel, a minimum of five coenological samples were carried out between 2001 and 2021. The sampling sizes were 2 m × 2 m; squares were randomly arranged within the plot. During the sampling, a total of 254 squares of vegetation were covered (a total of 1016 m^2); this was based on estimated percentage cover values of all vascular plant species occurring within the square. We used a cadastral map (1971, 2000), a topographic map (1984) and aerial photographs (1990, 2000) to determine the age of the abandoned lands. We also collected information from local farmers about each abandoned land, and validated these data using maps and aerial photographs.

2.3. Data Evaluation

The secondary succession of forest steppe species was assessed, considering the average total species number, relative cover values and diversity of the forest steppe species in the abandoned lands, as well as the coenosystematic classification of the forest steppe species. In addition, we examined how the habitat preferences (including the forest steppe category) and the coenosystemic classification of the species pool of each fallow type change during secondary succession. The Shannon index was used to calculate diversity. To characterize the succession stages, the habitat categories of the taxa included in the samples were evaluated based on the work of Simon [41], while their coenotaxons were based on the work of Borhidi [42]; these were then evaluated using group share calculation. When selecting the habitat preferences, we used the most typical habitat type for the species in the research area. In the case of coenotaxons, the main and subcategories were generally merged, with the exception of 5.3 for forest steppe species and its subcategories, and 8.4. and its subcategories. The 8.4.2. *Quercetalia pubescentis-petraeae* in Borhidi [42] was still classified by order, but in another publication [9] the syntaxon already represented a separate class called *Quercetea pubescentis-petraeae*. In the present publication, we applied the former classification.

To determine the range of forest steppe species, we used the work of Kun and Bölöni [15], but supplemented this with two further species with forest steppe behavior (*Chamaecytisus albus*, *Thesium lynophyllon*) (Table 1). According to the definition of Kun and Bölöni [15] in Hungary, forest steppe species are (1) dry and semi-dry grassland species that regularly appear in open-canopy forests, and (2) in the typically opened canopy forests, as well as species appearing at the edges of forests and shrubs. Previously, in the plant geography–vegetation literature, the species of point 2 were mostly considered to be forest steppe species, largely based on the categorization of Jakucs (1961). To compare our figures to Schmotzer's forest steppe data [37], we also signed the forest steppe species that occurred in the area based on Schmotzer's list (Table 1).The nomenclature of species follows the work of Simon [41] and that on coenotaxons by Borhidi [9,42].

Table 1. List of forest steppe species of the investigated abandoned lands (*—FS species determined by Schmotzer [37]).

1 *Anemone sylvestris* *	25 *Galium mollugo*	49 *Pulmonaria mollis* *
2 *Aster amellus*	26 *Geranium sanguineum* *	50 *Pulsatilla grandis*
3 *Aster linosyris*	27 *Hieracium bauhinii*	51 *Pyrus pyraster*
4 *Astragalus glycyphyllos*	28 *Hieracium cymosum*	52 *Quercus robur*
5 *Betonica officinalis* *	29 *Hypochoeris maculata* *	53 *Ranunculus polyanthemos* *
6 *Brachypodium pinnatum*	30 *Inula ensifolia*	54 *Rosa canina*
7 *Buglossoides purpureo-coer.*	31 *Inula hirta* *	55 *Rosa gallica* *
8 *Carex humilis* *	32 *Inula salicina*	56 *Salvia pratensis*
9 *Carex montana* *	33 *Iris variegata* *	57 *Sedum maximum* *
10 *Chamaecytisus albus* *	34 *Lathyrus lathifolius*	58 *Serratula tictoria*
11 *Cirsium pannonicum* *	35 *Lathyrus niger*	59 *Solidago virga-aurea*
12 *Clematis recta* *	36 *Lembotopis nigricans*	60 *Stachys recta*

Table 1. *Cont.*

13 *Colutea arborescens*	37 *Libanotis pyrenaica*	61 *Stipa pulcherrima*
14 *Crataegus monogyna*	38 *Linum flavum*	62 *Tanacetum corymbosum* *
15 *Crepis praemorsa* *	39 *Lychnis viscaria*	63 *Teucrium chamaedrys* *
16 *Doronicum hungaricum* *	40 *Origanum vulgare*	64 *Thesium linophyllon* *
17 *Echium maculatum*	41 *Peucedanum alsaticum* *	65 *Trifolium alpestre*
18 *Elymus hispidus*	42 *Peucedanum cervaria* *	66 *Trifolium montanum* *
19 *Euphorbia cyparissias*	43 *Poa angustifolia*	67 *Trifolium rubens*
20 *Euphorbia polychroma*	44 *Polygala major*	68 *Ulmus minor*
21 *Euphorbia virgata*	45 *Potentilla alba*	69 *Valeriana officinalis*
22 *Falcaria vulgaris*	46 *Potentilla argentea*	70 *Verbascum phoeniceum*
23 *Festuca rupicola*	47 *Prunella grandiflora*	71 *Vincetoxicum hirundinaria* *
24 *Filipendula vulgaris* *	48 *Prunus spinosa*	72 *Viola hirta*

The data were processed and visualized with PAleontological STatistics Version 4.08 (PAST), Oslo, Norway—alfa diversity module and multivariate, classical, hierarchical cluster analysis (the Unweighted Pair-Group Average (UPGMA) method with Euclidean similarity index) [43], MS Excel, and MS PowerPoint software packages (Microsoft Office Professional Plus 2016, Gödöllő, Hungary).

3. Results

3.1. Species Richness

A total of 72 forest steppe plant species were recorded in 254 sampling squares. Out of the 72, 53 species were included in surveys of abandoned vineyards, 35 in abandoned arable land, and 54 in abandoned grasslands.

In the case of abandoned vineyards, forest steppe species appeared even in the youngest fallows (12 species, Figure 1). In the second age group, their species numbers more than doubled (20 species), and in the second decade after abandonment, the number of FS species significantly increased, almost doubling (38 species). Even in the oldest age group, a small increase was observed in the number of species for the FS species (41 species). In the third decade after abandonment, forest steppe species accounted for almost a third (35%) of the total number of abandoned vineyards.

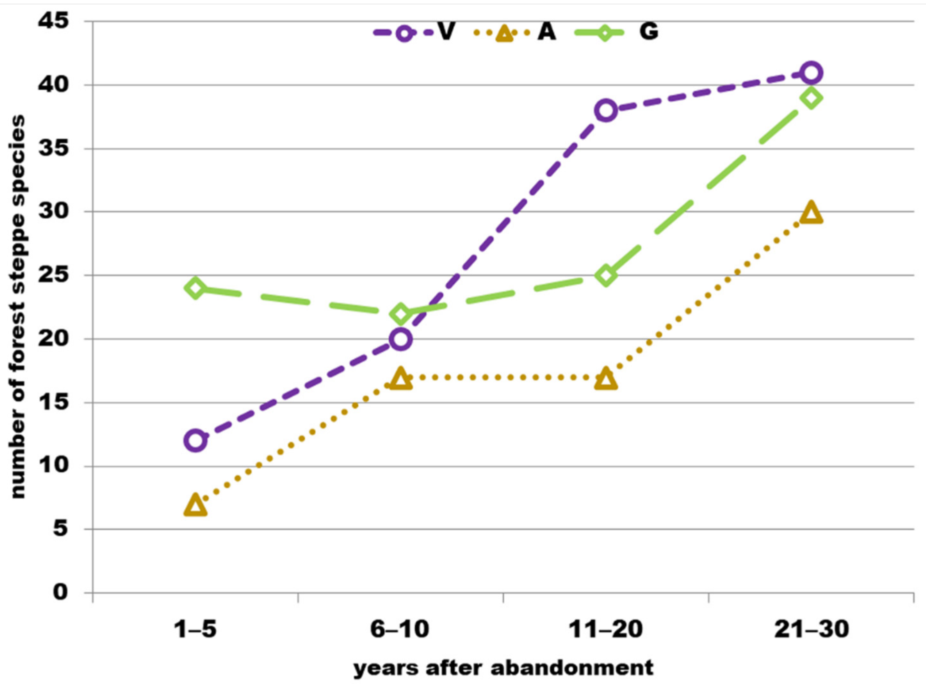

Figure 1. Changes in the total number of forest steppe species in the studied age groups of abandoned lands (V—vineyards, A—arable land, G—grasslands).

In the case of abandoned arable land, the number of FS species in the first age group was lower than in the case of vineyards (7 species, Figure 1). By the end of the first decade after abandonment, the number of FS species substantially increased, by 2.3-fold (17 species). In the second decade, the total number of FS species did not increase (17 species), and in the third decade after abandonment, a significant increase of 56% was observed (30 species). Almost one third (32.6%) of the species pool in mature old-fields accounted for forest steppe species.

In abandoned grasslands, the total number of FS species was very similar in the first decade (24 and 22 species, Figure 1). We noted that in the second decade after abandonment, three more FS species occurred (25 species). The number of FS species increased by nearly 64% in the last assessed decade (39 species). Due to the latter results, FS species accounted for half of the total number of species (51%).

3.2. Cover

In the youngest abandoned vineyards, the total cover of FS species was still very low (1.77%), but substantially increased by the end of the first decade (8.47%, Figure 2). In the second decade after abandonment, the total cover of FS species increased at a similar rate to that of Age 2 (15.26%). In the third decade, the total cover of FS species nearly doubled (31.82%), and their relative total cover further increased, as nearly 40% (42.42%) of abandoned vineyards were covered by forest steppe species (Figure 3).

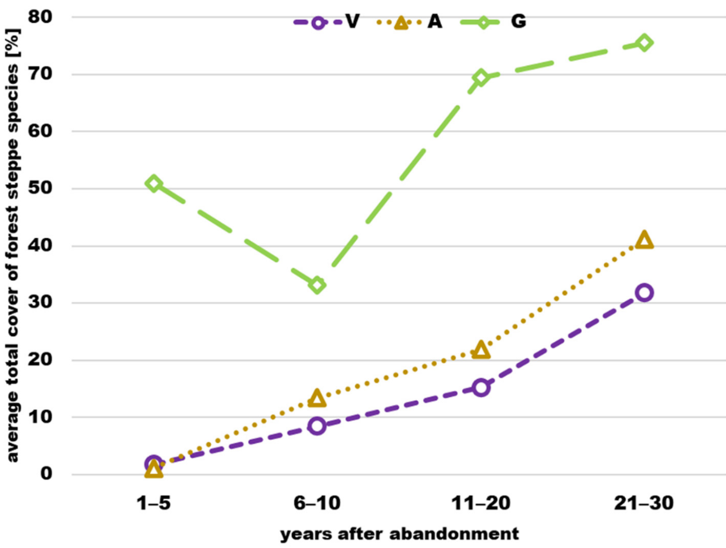

Figure 2. Changes in the average total cover of forest steppe species in different age groups of abandoned lands (V—vineyards, A—arable land, G—grasslands).

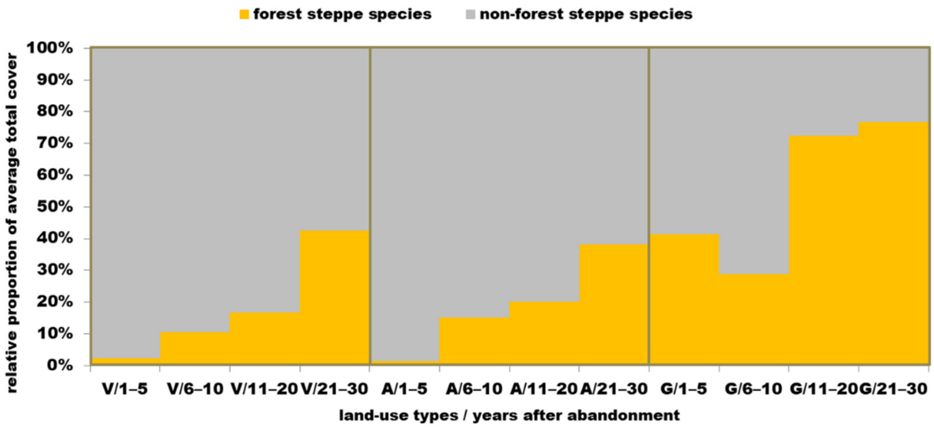

Figure 3. Changes in the relative proportion of average total cover of forest steppe species in different age groups of abandoned lands (V—vineyards, A—arable land, G—grasslands).

In abandoned arable land, the total cover of FS species in the youngest stands was similarly low to the youngest vineyard age group (1.1%, Figure 2). In the second abandoned age group, the total cover of FS species increased and significantly multiplied (13.43%). There was also a spectacular increase in total coverage; an almost three-fold increase (21.89%) was observed in the second decade after abandonment. In the third decade, the total cover of FS species (41.22%) and the relative share of this cover (38.1%) further increased; more than one third of the vegetation cover in old-fields of this age was FS species (Figure 3).

In abandoned grasslands, the total cover of FS species (50.98%) decreased by the end of the first decade (33.1%, Figure 2). In the second decade, the total cover of FS species more than doubled (69.51%). The increase was maintained in the last assessed decade, and their average total coverage increased by more than a third (75.58%) compared to Age 3. The relative average cover of the FS species in the latter age group accounted for more than three-quarters (76.73%) of the total cover (Figure 3).

3.3. Diversity

In abandoned vineyards, the Shannon diversity values of forest steppe species steadily increased after abandonment (Figure 4). The increase in FS species diversity was more uniform but smaller than the Shannon diversity calculated for all species in the plots; see [31]. Diversity increased the most (23%) in the second decade after abandonment.

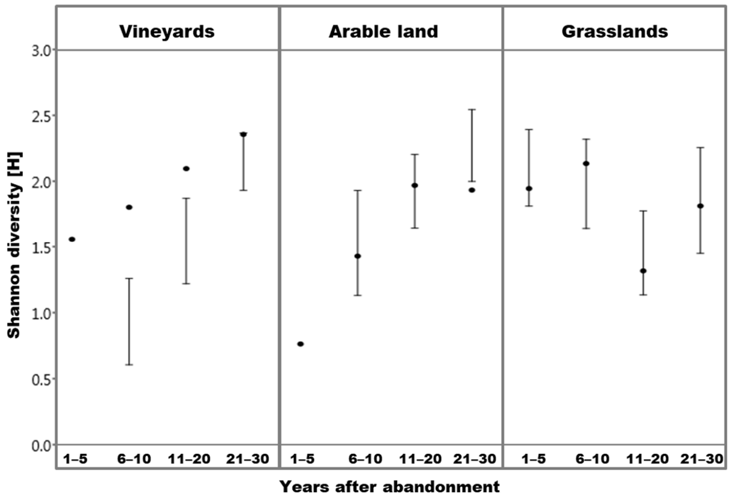

Figure 4. Shannon diversity values of forest steppe species in different age groups of abandoned lands (V—vineyards, A—arable land, G—grasslands).

In the case of arable land, the diversity of FS species significantly increased in the first two decades and then slightly declined (by 10%) in the third decade (Figure 4). The pattern of diversity in FS species is only partially consistent with the pattern of overall diversity, as the latter showed a smaller decline in the second decade [31], and Shannon diversity slightly decreased in the third decade after abandonment. Diversity increased the most (74%) in the first decade after abandonment.

In the case of abandoned grasslands, the diversity of FS species significantly fluctuated, as the initial small increase (16%) was followed by a significant decrease of nearly 60% (Figure 4). However, in the last decade after abandonment, the Shannon diversity of FS species increased by more than one-third again, which was the most significant increase during the studied period. The pattern of diversity in Age 2 differs from the Shannon diversity value calculated for all species—see [31]—as only a slight decrease was observed for FS species during this period.

In the case of abandoned lands, the initial (age group 1) Shannon-diversity values were 1.55, 0.8 and 1.9 for vineyards, arables and grasslands, respectively. In the third decade after abandonment (age group 4), these diversity values changed to 2.36, 1.8 and 1.8 for vineyards, arables and grasslands, respectively.

3.4. Habitat Preference

In abandoned vineyards, most species in Age 1 belong to the 'disturbed habitats' group, followed by 'hey meadows pasture grasslands', 'forest steppe' and 'dry grasslands' species (Figure 5). The 'dry grasslands' species are the most abundant in Age 2. In this age group, 'forest steppe' species were the second most common, while 'hey meadows' were third, followed by 'disturbed habitats'. The latter were only sub-dominant in the second half of the first decade following abandonment. The proportion of 'forest steppe' species that are dominant in Age 3 almost doubled. The number of the second most common 'dry grasslands' species was minimal, while the proportion of the third 'hey meadows' species decreased slightly more than that of the former. In Age 4, 'forest steppe' species dominated, showing a minimal but continued increase in proportion. This was trailed by 'dry grasslands', followed by 'hey meadows', with 'disturbed habitats' showing a minimal but declining proportion, taking fourth place.

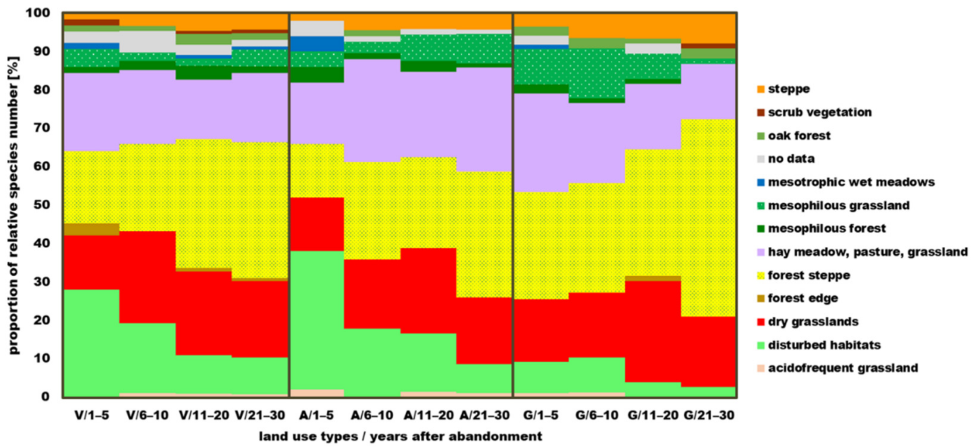

Figure 5. Distribution of the relative species number of habitat category in different age groups of abandoned lands (V—vineyards, A—arable land, G—grasslands).

In abandoned arable land, most species were in the 'disturbed habitats' category (36%), with the second most common landing in the 'hey meadows' category (16%), while the third most common species belong to the 'forest steppe' and 'dry grasslands' groups (Figure 5). Age 2 is dominated by the 'hey meadows' species, but the 'forest steppe' species are almost co-dominant, and 'dry grasslands' and 'disturbed habitats' are sub-dominant. The 'forest steppe' species are the most abundant in Age 3, while the 'dry grassland' and 'hey meadows' groups are almost co-dominant, followed by the declining 'disturbed habitats' category. Age 4 is also dominated by 'forest steppe' species, followed by 'hey meadows', 'dry grasslands' and 'disturbed habitats'.

In grasslands, 'hey meadows' and 'forest steppe' species are dominant in Age 1, followed by 'dry grasslands' and 'mesophilous grasslands' (Figure 5). In Age 2, the 'forest steppe' clearly dominates, and the species in the 'hey meadows', 'dry grasslands' and 'mesophilous grasslands' groups are significant. In Age 3, 'forest steppe' dominates, followed by the sub-dominant 'dry grasslands', and then 'hay meadows' and 'steppe' trees. In Age 4, 'forest steppe' species predominate in terms of proportion, followed by 'dry grasslands', 'hay meadows' and 'steppe' species.

In abandoned vineyards, the 'dry grasslands' species showed the highest relative cover in the youngest age group, which overlays almost two-thirds of the total cover (Figure 6). In this age group, 'disturbed habitats' species still form a great extent of the total cover, while the relative cover of 'forest steppe' species was just over 2.2%. By the second half of the first decade, the proportion of 'dry grasslands' species minimally declined, while that of 'disturbed habitats' more significantly declined, by a third. In contrast, the share of 'forest steppe' species increased by almost fivefold (ca. 8%), and the proportion of species in the 'hay meadows, pasture, grassland' group also significantly increased. In the second decade following abandonment, the proportion of dominant 'dry grasslands' changed a little, and the proportion of sub-dominant 'forest steppe' nearly doubled, while the share of two other groups, 'hay meadow, pasture, grassland' and 'mesophilous forest', was around 5%. In the oldest age group, the 'forest steppe' species became dominant, the proportion of 'dry grasslands' species decreased, and the 'dry grasslands' species showed a decline by almost half. In addition to these groups, the share of the third-largest, 'hay meadow, pasture, grassland', was over 10%.

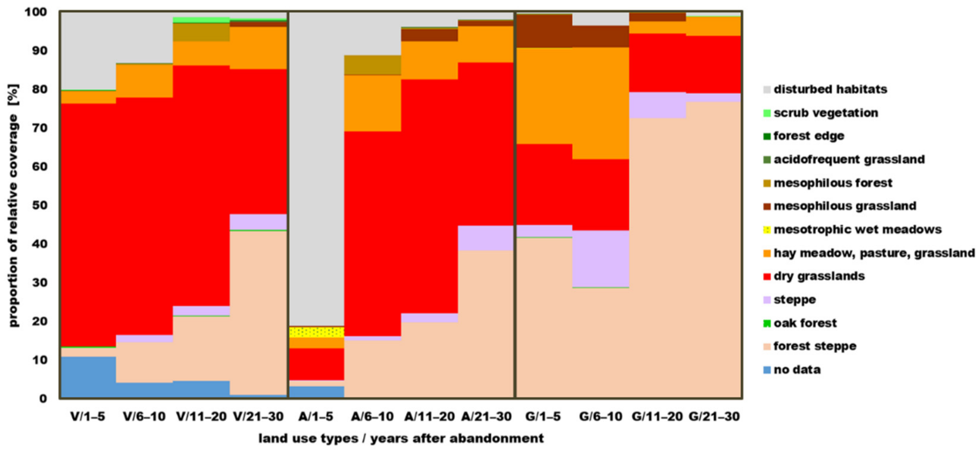

Figure 6. Distribution of the relative coverage of habitat category in different age groups of abandoned lands (V—vineyards, A—arable land, G—grasslands).

In the youngest abandoned old-fields, the relative cover of the dominant 'disturbed habitats' species is more than 80%, while that of the second highest proportion of 'dry grasslands' is less than 10% (Figure 6). The shares of 'hay meadows, pasture, grassland' and the fourth highest proportion of 'forest steppe' species (1.43%) are also above 1%. In Age 2, the 'dry grassland' species became dominant, but the proportion of 'hay meadows, pasture, grassland', 'forest steppe', 'steppe' and 'mesophilous forest' species also significantly increased. In contrast, in the previous age group, the proportion of the still-dominant 'disturbed habitats' species significantly declined. In the second decade, in addition to the dominant 'dry grasslands' and the already sub-dominant 'forest steppe' species, the proportion of 'mesophilous grassland' only increased by a few percentage points, while the most spectacular decrease was observed in the proportion of 'disturbed habitats' species. Despite the declining relative cover of Age 4, the 'dry grasslands' species remained dominant, but the share of sub-dominant 'forest steppe' rose to 38%. The proportion of 'steppe' and 'hay meadows, pasture, grassland' species was also significant in the oldest abandoned arable land.

In the case of the youngest abandoned grasslands, in addition to the dominant 'forest steppe' species, the proportion of two other habitat categories, 'hay meadows, pasture, grassland' and'dry grasslands', is around 20% (Figure 6). The share of 'mesophilous grassland' is also higher than in Age 1. The highest proportion of the three habitat categories in Age 1 is also characteristic of that in Age 2, but 'hay meadows, pasture, grassland' 'and forest steppe' species are already co-dominant, with the highest proportion. In the second decade after abandonment, the 'forest steppe' species slightly increased, regaining their dominant status. In the first decade, the proportion of the other three most-covered habitat categories decreased. The proportion of 'steppe' recently decreased, and that of 'dry grasslands' decreased by a few percent.The species of 'hay meadows, pasture, grassland'had a significant decrease to nearly with twenty percent. In the oldest grasslands, the 'forest steppe' species were clearly monodominant, further increasing their proportion.

The ratio of the second highest proportion of 'dry grasslands' species is less than 15%, while the proportion of disturbed habitats was almost zero.

3.5. Coenosystematical Analysis

3.5.1. Coenosystematical Characteristics of Abandoned Lands

Based on the average relative species numbers, the number of indifferent elements was the highest in the studied abandoned lands, except for two age groups (Table 2). Most indifferent species occurred in the A1–5 and A11–20 groups, while the fewest occurred in the G11–20, G21–30 groups. There is an overall decreasing trend in the distribution of indifferent species between age groups. After the indifferent species, the species of the *Festuco-Brometea* class were the most abundant in two-thirds of the age groups. In the case of the two oldest grasslands, the species numbers of the aforementioned two categories were the same or almost the same. The share of *Molinio-Arrhenatheretea*, *Querco-Fagetea*, *Quercetalis pubescentis-petraea* and *Festucetalia valesiaceae* was also significant, accounting for about half of the age groups in 2–4., the most abundant category. The *Festuco-Brometea* and *Festucetalia valesiaceae* elements were found in the smallest relative species in A1–5 and V1–5, while the highest relative species were found in G11–20, G21–30 and V21–30.

Table 2. Relative proportion of coenosystamatical groups of the species in abandoned lands (V—vineyards, A—arable land, G—grasslands, 1.5.1 *Phragmitetalia*, 3.3 *Chenopodietea*, 3.4 *Secalietea*, 3.5 *Artemisietea*, 3.6.1.1 *Convolvulo-Agropyrion*, 3.7 *Plantaginetea*, 3.8.1 *Agrostietalia stoloniferae*, 3.9.1 *Oryzetalia*, 5.1.1 *Nardetalia*, 5.2 *Sedo-Scleranthetea*, 5.3. *Festuco-Brometea*, 5.3.1 *Festucetalia valesiacae*, 5.3.1.1 *Festucion valesiacae*, 5.3.1.4 *Bromo-Festucion pallentis*, 5.3.3.1 *Festucion vaginatae*, 5.3.3.2 *Bromion tectorum*, 5.4 *Molinio-Arrhenatheretea*, 5.5 *Festuco-Puccinellietea*, 6.2 *Epilobietea angustifolii*, 8.1.1 *Salicetalia purpureae*, 8.3. *Quercetea robori-petraeae*, 8.4 *Querco-Fagetea*, 8.4.1, 8.4.2 *Quercetalia pubescentis-petraeae*, 8.4.2.2 *Orno-Ostryon*, 8.4.2.3 *Aceri tatrico-Quercion*, 8.4.2.4 *Quercion petraeae-cerris*, 8.4.3 *Fagetalia*, 8.4.3.2 *Carpinion betuli*, 8.6.1 *Prunetalia spinosae*, Indiff. Indifferent, n.d. no data).

Coeno. Groups	Land-Use Types/Years after Abandonment											
	V/1–5	V/6–10	V/11–20	V/21–30	A/1–5	A/6–10	A/11–20	A/21–30	G/1–5	G/6–10	G/11–20	G/21–30
1.5.1	0.00	0.00	0.00	0.00	1.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3.3	4.62	2.25	1.77	0.85	3.77	2.82	2.67	1.05	1.14	2.53	2.67	1.23
3.4	3.08	3.37	0.88	1.69	5.66	4.23	1.33	1.05	3.41	0.00	0.00	1.23
3.5	4.62	3.37	3.54	1.69	3.77	1.41	4.00	1.05	3.41	1.27	2.67	1.23
3.6.1.1	1.54	1.12	0.88	0.85	1.89	1.41	1.33	1.05	1.14	1.27	1.33	1.23
3.7	1.54	0.00	0.00	0.00	1.89	0.00	0.00	0.00	1.14	0.00	0.00	0.00
3.8.1	0.00	1.12	0.00	0.85	0.00	0.00	0.00	1.05	0.00	1.27	0.00	1.23
3.9.1	0.00	0.00	0.00	0.00	1.89	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5.1.1	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00	1.14	0.00	0.00	0.00
5.2	3.08	1.12	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5.3.	1.54	13.48	17.70	19.49	3.77	14.08	9.33	9.47	10.23	12.66	26.67	22.22
5.3.1	3.08	5.62	7.08	10.17	0.00	8.45	6.67	8.42	7.95	5.06	9.33	8.64
5.3.1.1	0.00	0.00	0.00	0.85	0.00	0.00	0.00	0.00	0.00	0.00	2.67	3.70
5.3.1.4	0.00	0.00	0.88	0.85	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5.3.3.1	0.00	1.12	0.88	0.85	0.00	0.00	0.00	0.00	0.00	0.00	1.33	1.23
5.3.3.2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.05	0.00	0.00	0.00	0.00
5.4	7.69	4.49	4.42	5.93	1.89	7.04	6.67	12.63	11.36	12.66	8.00	2.47
5.5	1.54	1.12	1.77	1.69	3.77	4.23	2.67	3.16	1.14	3.80	2.67	2.47
6.2	1.54	1.12	0.88	0.85	1.89	0.00	1.33	0.00	1.14	0.00	0.00	1.23
8.1.1	1.54	1.12	0.88	0.85	0.00	1.41	0.00	0.00	1.14	0.00	1.33	0.00
8.3.	3.08	1.12	1.77	1.69	0.00	1.41	1.33	1.05	2.27	0.00	1.33	0.00
8.4	6.15	3.37	7.08	5.08	5.66	5.63	4.00	5.26	5.68	5.06	4.00	11.11
8.4.1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.27	0.00	0.00
8.4.2	6.15	3.37	7.08	5.08	5.66	5.63	4.00	5.26	5.68	5.06	4.00	11.11
8.4.2.2	0.00	0.00	0.00	0.85	0.00	1.41	1.33	1.05	1.14	0.00	1.33	0.00
8.4.2.3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.14	0.00	0.00	0.00
8.4.2.4	0.00	0.00	1.77	1.69	0.00	1.41	0.00	2.11	2.27	2.53	0.00	1.23
8.4.3	1.54	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8.4.3.2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.33	0.00
8.6.1	0.00	1.12	0.88	0.85	0.00	0.00	0.00	1.05	1.14	0.00	1.33	4.94
Indiff.	44.62	43.82	36.28	35.59	50.94	39.44	52.00	43.16	34.09	45.57	26.67	23.46
n.d.	3.08	6.74	3.54	0.85	5.66	0.00	1.33	1.05	2.27	0.00	1.33	0.00

Examining the relative cover of fallows, elements in the indifferent category, then the *Festuco-Brometea* and *Festucetalia valesiaceae* categories, predominate in most age groups (Table 3). In contrast, *Salicetalia purpureae* has the second highest relative total cover value for V1–5. In half of the examined abandoned lands, including the first three age groups of vineyards and arable lands, indifferent elements clearly dominate. In the other half of the abandoned areas, including the oldest vineyards, arable land and grassland plots, *Festuco-Brometea*, *Festucetalia valesiaceae* and *Quercetalis pubescentis-petraeae* showed the highest coverage of coenotaxones.

Table 3. Relative average cover of coenosystamatical groups of the species of abandoned lands (V—vineyards, A—arable land, G—grasslands) 1.5.1 *Phragmitetalia*, 3.3 *Chenopodietea*, 3.4 *Secalietea*, 3.5 *Artemisietea*, 3.6.1.1 *Convolvulo-Agropyrion*, 3.7 *Plantaginetea*, 3.8.1 *Agrostietalia stoloniferae*, 3.9.1 *Oryzetalia*, 5.1.1 *Nardetalia*, 5.2 *Sedo-Scleranthetea*, 5.3. *Festuco-Brometea*, 5.3.1 *Festucetalia valesiacae*, 5.3.1.1 *Festucion valesiacae*, 5.3.1.4 *Bromo-Festucion pallentis*, 5.3.3.1 *Festucion vaginatae*, 5.3.3.2 *Bromion tectorum*, 5.4 *Molinio-Arrhenatheretea*, 5.5 *Festuco-Puccinellietea*, 6.2 *Epilobietea angustifolii*, 8.1.1 *Salicetalia purpureae*, 8.3. *Quercetea robori-petraeae*, 8.4 *Querco-Fagetea*, 8.4.1, 8.4.2 *Quercetalia pubescentis-petraeae*, 8.4.2.2 *Orno-Ostryon*, 8.4.2.3 *Aceri tatrico-Quercion*, 8.4.2.4 *Quercion petraeae-cerris*, 8.4.3 *Fagetalia*, 8.4.3.2 *Carpinion betuli*, 8.6.1 *Prunetalia spinosae*, Indiff. Indifferent, n.d. no data).

Coeno. Groups	Land-Use Types/Years after Abandonment											
	V/1–5	V/6–10	V/11–20	V/21–30	A/1–5	A/6–10	A/11–20	A/21–30	G/1–5	G/6–10	G/11–20	G/21–30
1.5.1	0.00	0.00	0.00	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3.3	0.36	0.55	0.02	0.03	0.19	2.81	0.11	0.03	0.15	0.09	0.10	0.01
3.4	0.14	0.33	0.04	0.15	1.60	2.77	1.64	0.16	0.67	0.00	0.00	0.01
3.5	0.27	1.87	0.67	0.93	0.09	0.07	0.35	0.02	1.29	0.32	0.01	0.25
3.6.1.1	0.11	0.19	0.05	0.13	0.87	0.62	0.14	0.01	0.16	0.02	0.01	0.95
3.7	0.01	0.00	0.00	0.00	0.10	0.00	0.00	0.00	0.05	0.00	0.00	0.00
3.8.1	0.00	0.02	0.00	0.45	0.00	0.00	0.00	0.01	0.00	8.41	0.00	0.76
3.9.1	0.00	0.00	0.00	0.00	0.32	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5.1.1	0.00	0.00	0.00	0.18	0.00	0.00	0.00	0.00	0.11	0.00	0.00	0.00
5.2	0.09	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5.3.	0.00	8.45	23.61	17.71	0.41	20.57	16.44	17.69	18.61	8.49	61.49	58.79
5.3.1	0.03	4.29	5.03	20.51	0.00	11.14	5.88	23.78	23.19	17.02	22.77	6.80
5.3.1.1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.51	0.20
5.3.1.4	0.00	0.00	1.69	0.18	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
5.3.3.1	0.00	0.08	0.77	0.84	0.00	0.00	0.00	0.00	0.00	0.00	3.69	2.21
5.3.3.2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00
5.4	0.70	0.65	0.69	2.20	0.08	1.00	3.89	3.75	17.05	10.75	2.28	0.46
5.5	0.09	0.09	0.34	0.32	0.10	2.35	9.88	4.67	0.65	0.49	0.92	0.65
6.2	0.00	0.04	0.02	0.11	0.08	0.00	0.07	0.00	0.10	0.00	0.00	0.19
8.1.1	10.94	4.16	4.52	1.05	0.00	0.01	0.00	0.00	1.74	0.00	0.01	0.00
8.3.	0.98	0.04	0.40	0.09	0.00	0.12	0.08	0.10	0.09	0.00	0.07	0.00
8.4	0.50	0.17	0.37	0.37	0.00	0.00	0.00	0.13	0.27	0.23	0.33	2.67
8.4.1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00
8.4.2	1.14	3.42	0.40	5.76	1.23	0.54	4.48	1.46	0.80	6.04	1.82	13.07
8.4.2.2	0.00	0.00	0.00	0.00	0.00	0.12	0.09	0.01	0.11	0.00	0.01	0.00
8.4.2.3	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00
8.4.2.4	0.00	0.00	0.52	3.05	0.00	0.19	0.00	0.43	2.98	1.86	0.00	1.70
8.4.3	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
8.4.3.2	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.00
8.6.1	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.38
Indiff.	84.66	75.33	60.33	46.28	90.76	57.55	57.31	47.62	32.32	46.54	4.48	10.42
n.d.	0.01	0.10	0.54	0.09	3.27	0.00	0.01	0.02	0.04	0.00	0.01	0.00

3.5.2. Coenosystematical Characteristics of Forest Steppe Species

In abandoned vineyards, most forest steppe species in Age 1 belong to the *Quercetalia pubescentis-petraeae* group. This is followed by the indifferent category, and then the *Festucetalia valesiacae* species (Figure 7). FS species in the *Festuco-Brometea* category have not yet appeared in this age group. The 'indifferent' FS species are the same in Age 2. The second most common species in this age group belonded to three groups: *Festuco-Brometea*, *Festucetalia valesiacae*, and *Quercetalia pubescentis-petraeae*. In addition, *Querco-Fagetea* FS species also accounted for a larger share (10%). In Age 3, FS species from the *Festuco-Brometea*, *Quercetalia pubescentis-petraeae* and indifferent groups dominated, followed by *Festucetalia valesiacae*. In Age 4, *Festuco-Brometea* FS species were dominant, with their proportion continuing to increase over time. This was followed by the indifferent category and the *Festucetalia valesiacae* group.

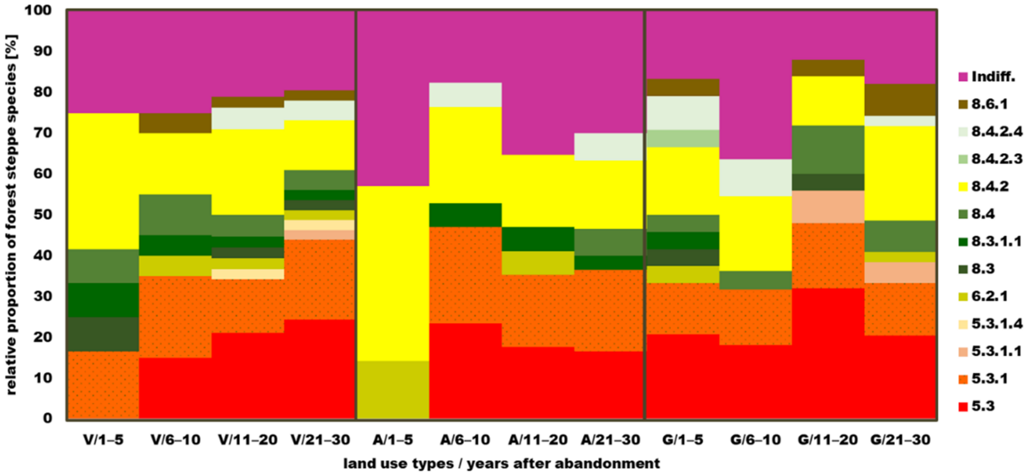

Figure 7. Relative proportion of coenosystamatical groups of forest steppe species in different age groups of abandoned lands (V—vineyards, A—arable land, G—grasslands, Indiff.—indifferent, 8.6.1—*Prunetalia spinosae*, 8.4.2.4—*Quercion petraeae-cerris*, 8.4.2.3—*Aceri tatarico-Quercion*, 8.4.2—*Quercetalia pubescentis-petraeae*, 8.4—*Querco-Fagetea*, 8.3.1.1—*Quercion robori-petraeae*, 8.3—*Quercetea robori-petraeae*, 6.2.1—*Epilobietalia angustifolii*, 5.3.1.4—*Bromo-Festucion pallentis*, 5.3.1.1—*Festucion valesiacae*, 5.3.1—*Festucetalia valesiacae*, 5.3—*Festuco-Brometea*).

In the case of arable land, most forest steppe species in Age 1 belong to the *Quercetalia pubescentis-petraeae* and its co-dominant indifferent (Figure 7) category. These are followed by FS elements in the *Atropetalia* group. In Age 2, *Festuco-Brometea*, *Festucetalia valesiacae* and *Quercetalia pubescentis-petraeae* have the highest share of the FS elements. FS species in the indifferent categories have the second highest proportions. In Age 3, indifferent FS species predominate, followed by *Festuco-Brometea*, *Festucetalia valesiacae*, and *Quercetalia pubescentis-petraeae*. In Age 4, a similar distribution can be observed as for the groups mentioned in Age 3; however, the proportion of indifferent FS species in the oldest analyzed age group is lower than it was in the second decade after abandonment.

In the case of abandoned grasslands, in Age 1, most FS species belong to the *Festuco-Brometea* class, while the second largest FS species belong to the categories *Quercetalia pubescentis-petraeae* and indifferent species (Figure 7). These are followed by the FS elements of the *Festucetalia valesiacae* and *Quercetalia pubescentis-petraeae* groups. In Age 2, the proportion of indifferent FS species is the highest, followed by that of *Festuco-Brometea* and *Quercetalia pubescentis-petraeae*. In Age 3, the FS elements of the *Festuco-Brometea* class dominate, and *Festucetalia valesiacae* is sub-dominant. The FS species of the *Querco-Fagetea*, *Quercetalia pubescentis-petraeae* and indifferent category are almost equal, and the third most-abundant. In Age 4, the proportion of FS elements in *Quercetalia pubescentis-petraeae* is highest, followed by *Festuco-Brometea,* with a slightly smaller share. The indifferent FS species number is the third highest in the oldest fallows, followed by the *Festucetalia valesiacae* group.

In abandoned vineyards, FS species classified in the *Quercetalia pubescentis-petraeae* group showed the highest average total cover in Age 1, followed by *Quercetea robori-petraeae*, and *Quercion robori-petraeae*. The values of the indifferent category are low (3.95%) (Figure 8). The *Festuco-Brometea* category does not appear in this age group. In Age 2, *Festuco-Brometea* elements are co-dominant in the *Quercetalia pubescentis-petraeae* FS species coverage. The *Festucetalia valesiacae* FS species cover is sub-dominant and the indifferent category formed only 8.38% of the total proportion. In Age 3, the coverage of FS species classified in the *Festuco-Brometea* group is highly dominant, followed by the *Festucetalia valesiacae* and *Bromo-Festucion pallentis* categories. The coverage of indifferent FS species represents the 4th most abundant category. The abundance of *Quercetalia pubescentis-petraeae* FS species is minimal in this age group (2.4%). In Age 4, the cover of FS elements of the *Festucetalia valesiacae* category predominates (40.1%), while *Festuco-Brometea* species are sub-dominant. The average total cover of *Quercetalia pubescentis-petraeae* and indifferent FS is almost the same.

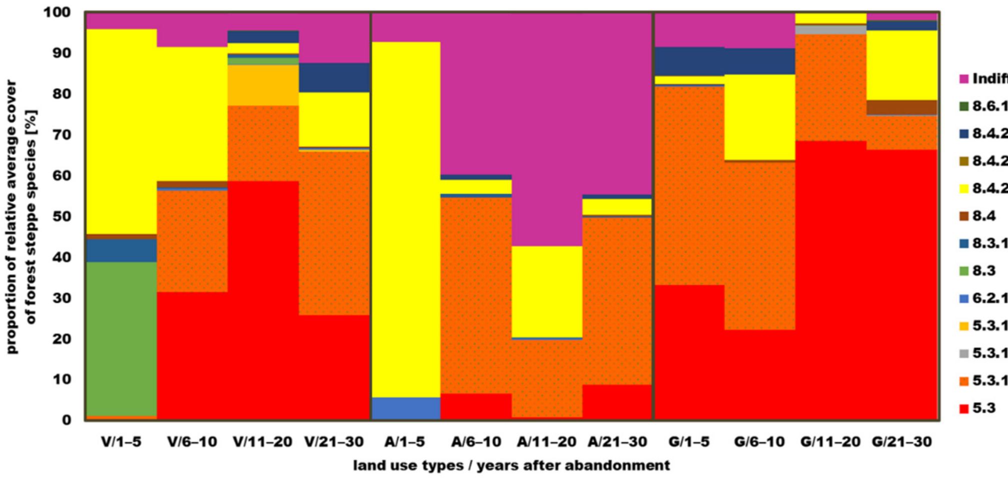

Figure 8. Relative average cover of coenosystamatical groups of forest steppe species in different age groups of abandoned lands (V—vineyards, A—arable land, G—grasslands, Indiff.—indifferent, 8.6.1—*Prunetalia spinosae*, 8.4.2.4—*Quercion petraeae-cerris*, 8.4.2.3—*Aceri tatarico-Quercion*, 8.4.2—*Quercetalia pubescentis-petraeae*, 8.4—*Querco-Fagetea*, 8.3.1.1—*Quercion robori-petraeae*, 8.3—*Quercetea robori-petraeae*, 6.2.1—*Epilobietalia angustifolii*, 5.3.1.4—*Bromo-Festucion pallentis*, 5.3.1.1—*Festucion valesiacae*, 5.3.1—*Festucetalia valesiacae*, 5.3—*Festuco-Brometea*).

In abandoned arable lands, the highest average total cover in Age 1 is, surprisingly, found in the FS species of the group *Quercetalia pubescentis-petraeae* (Figure 8). The latter is followed by the cover values of the FS species classified as indifferent and *Atropetalia*. The FS species of *Festuco-Brometea* and *Festucetalia valesiacae* appeared only in Age 2, with the latter one being dominant. Indifferent FS species are sub-dominant, while the FS species cover of *Quercetalia pubescentis-petraeae* significantly decreased. In Age 3, the cover values of indifferent FS species are the highest. The abundance ratios of *Festucetalia valesiacae* and *Quercetalia pubescentis-petraeae* FS are very similar (18.8 and 22.2%, respectively), with the latter having an increased coverage ratio compared to Age 2. In this age group, *Festuco-Brometea* FS elements are present with a very minimal value. In Age 4, the total cover of indifferent FS species continues to dominate, while *Festucetalia valesiacae* is the second most abundant type. The proportion of *Festuco-Brometea* FS elements is higher than those of the second age group. The coverage of *Quercetalia pubescentis-petraeae* FS elements is strongly reduced.

In abandoned grasslands, FS elements classified in the *Festucetalia valesiacae* group showed the highest average total cover in Age 1. The FS species of *Festuco-Brometea* are sub-dominant. The proportion of FS species in *Quercion petraeae-cerris* and indifferent was similar, at around 10%. In Age 2, the FS elements of the *Festucetalia valesiacae* were dominant. *Festuco-Brometea* and *Quercetalia pubescentis-petraeae* categories have the second higher values. This is followed by the total cover of the indifferent FS species. The cover share of FS species in the *Quercion petraeae-cerris* group is very similar to that in Age 1. In Age 3, *Festuco-Brometea* FS elements have the highest average total coverage. The proportion of FS elements in *Festucetalia valesiacae* and *Quercetalia pubescentis-petraeae* decreases in this age group, while the proportion of indifferent FS species is almost zero. In Age 4, *Festuco-Brometea* FS elements continue to dominate, with the coverage ratio of *Quercetalia* *pubescentis-petraeae* FS elements increasing, resulting in their becoming the second most abundant category.

3.6. Multivariate Analysis

Based on the results of the multivariate analysis (hierarchical cluster analysis—UPGMA) of the studied abandoned sites, the grasslands are clearly separated, while almost all the arable lands and vineyards form a well-defined group (Figure 9), showing a kind of trajectory following abandonment.

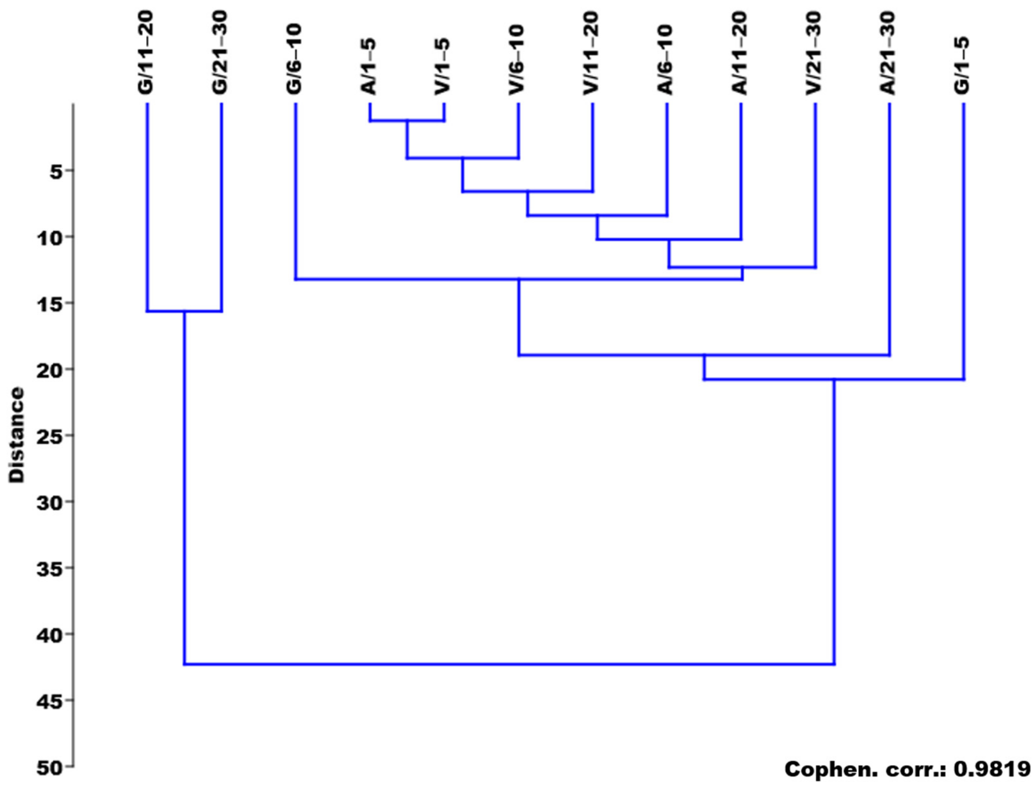

Figure 9. Results of the hierarchical cluster analysis of forest steppe species in different age groups of abandoned lands (V—vineyards, A—arable land, G—grasslands).

4. Discussion

4.1. Species Richness

A total number of 72 forest steppe species (Table 1) were recorded in the coenological surveys based on the FS list of Kun and Bölöni [15], which is more than one and half times higher than the number of those found by Schmotzer (42 species) [37] in a nearby microregion (Heves–Borsodi Plain) (Table 1). The discrepancy is due to the differences in the definition of FS species (cf. Materials and Methods section) and the size and historical history of the studied areas. When regenerating abandoned lands, fewer FS species can be expected than when studying semi-natural vegetation, as a significant proportion of FS species in the latter case belong to the coenological categories of *Festuco-Brometea*, *Festucetalia valesiacae* and *Quercetalia pubescentis-petraeae*. These are not indifferent, but generalist or sensitive species. The number of forest steppe species in abandoned vineyards steadily increased in the studied age groups (Figure 1). In the vineyards, the species growth curve for the forest steppe species was similar to the increase in the total species number of the area—see [31]—but the colonization of FS species was greater than the increase in the total species number in the second decade after abandonment. One of the main reasons for the latter result was that *Calamagrostis* has already occurred in several squares, with low values regarding coverage in older abandoned vineyards [31], which favored the more abundant appearance of forest steppe species (e.g., *Brachypodium pinnatum*, *Inula ensifolia*, *Stipa pulcherrima*). This trend has already been observed by other researchers [44–46].

The number of forest steppe species in abandoned arable land, such as vineyards, also steadily increased (Figure 1). The increase in the total number of species in the FS species was very similar to the increase in the total number of species in the analyzed old-fields; see [31]. An increase in species richness in the vegetation of regenerating arable land was reported by other studies [47–49]. The increase in the number of FS species in the fields was not uniform, as it was only small in the second decade after abandonment, similar to the total number of species [31]. Due to the small size of the plots, forest steppe species of the former hedges and remaining, species-rich, semi-natural patches can more easily colonize the abandoned old-fields, accelerating the initial process of secondary succession, similar to the observations of other researchers [45,48,49].

The total number of forest steppe species of former pastures and meadows (grasslands) did not decrease during the observed abandonment period; instead, they slightly increased, and then significantly increased from the second decade onwards (Figure 1). This result shows an exact opposite trend in the change of the total number of abandoned grasslands species; see [31]. The increase or stagnation in the species richness of abandoned pastures has been confirmed by other researchers [50–52]. Chen et al. (2005) found that the number of species increased compared to both non-grazed and intensively grazed areas [52]. In contrast, others have observed a decrease in the number of species in grasslands over time, following abandonment [53–56]. For decades, exclusion from grazing in the barely grazed stand of the near-natural loess grassland caused only minor floristic and structural changes. In the previously continuously grazed degraded stand, the enclosure led to a drastic decrease in the number of species, cover and phytomass, and resulted in significant coenological differences [57].

These differences may be due to the fact that, in addition to the grazing rate, environmental factors also affect species richness; grazing shows a species-increasing effect, in addition to productive site factors, but species richness decreases in low-productivity, dry sites [58–60]. If nutrients and light are the main limiting factors, grazing increases the number of species, but if the amount of water that can be absorbed is the main limiting factor, grazing has a species-reducing effect [58,59].

The decline in the total number of species does not appear to affect the number of forest steppe species, and new forest steppe species have settled in place of the disappearing species.

In the third decade after abandonment, most FS species were found in abandoned vineyards, but their opulence was almost the same in abandoned grasslands. Of the three studied types, the fewest FS species were typical of abandoned arable land. Based on the curve (Figure 1), the number of forest steppe species was not saturated in either the arable lands or the grasslands, so a further increase in the total number of species is expected for both types, even after 30 years. In the case of vineyards, the total FS species number will be close to equilibrium in three decades.

4.2. Cover

In the case of vineyards, the relative cover of the forest steppe species steadily increased (Figure 2). Their relative species growth was higher in the oldest studied age group (Figure 3). The increase in the total cover of FS species is less spectacular than the increase in the number of species (Figure 1), indicating that their relatively quick colonization after their relatively rapid establishment is a time-consuming process. The latter is supported by the fact that the increase in the total cover of FS species was greatest in the third decade after abandonment.

In the case of arable land, the absolute and relative total cover of FS species steadily increased, as was in the case in vineyards (Figures 2 and 3). The rate of cover growth in abandoned arable land, such as vineyards, was much smaller than the increase in species number (Figure 1). Growth was not the same in all periods, as it was both absolute and relatively higher in the second decade after abandonment than in the other periods. The slower growth of total cover, in addition to the aforementioned reasons for vineyards, is influenced by the cover of species with a strong competitive capacity [47,61].

In abandoned grasslands, the change in the total cover of FS species differed from the increase in their species number (Figure 1) and the other two types (Figures 2 and 3). A decrease in the total cover of FS species was only observed in this type in the second half of the first decade after abandonment. The more significant decrease in the average total cover of the G/6–10 FS species compared to the values of G/1–5 (contrary to the trends observed in the old-fields and vineyards, for example) can mainly be explained by the condition of the neighboring lands and the slightly different habitat conditions. We consider it important to note that the number of FS species decreased by only two compared to the previous age group (Figure 1). The first parcel of the G/6–10 group is in contact with a vineyard that is still under cultivation, and an arable land that was abandoned a few years ago, with a dirt road running nearby. This plot is the smallest of the abandoned grasslands. *Brachypodium pinnatum* alone is absent in this plot, with *Calamagrostis epigeios* dominating in most of the samplings. The latter phenomenon is presumably due to the vegetation of adjacent plots, the smaller size of the plot, and the succession-slowing behavior of *Calamagrostis* [31,45]. In one sampling in the first parcel of land, the coverage of *Trifolium rubens* was the highest of the FS species, at 90%, and *Calamagrostis* had a coverage value of only 5% in this quadrat. Furthermore, in another plot in the age group, only 2 of the 5 quadrats had *Brachypodium*, with relatively low (5 and 15%) cover values. *Vicia cracca*, on the other hand, was dominant or co- or sub-dominant in most of the samplings. The latter phenomenon can be traced back to the slightly more xerophilic nature of the plot and the vegetation of the adjacent plots. It is true for both plots that the vegetation of the adjacent areas is less rich in FS species than in other grasslands. The phenomenon of interspecific competition is observed in the abundance values of the more sensitive FS species, *Calamagrostis* and *Vicia cracca*. The latter two species may be in strong competition for colonization of *Brachypodium pinnatum* or the more sensitive FS species. The more degraded stands, which are out of equilibrium, react violently even to small interventions, such as abandoning grazing, which leads to degradation and a decrease in the species pool [29]. In the case of abandoned vineyards and arable land, there is no significant decline in the FS cover values of the first and second age groups because the initial situation there is quite different. On an almost-nudum surface, FS species need to colonize and disperse in the first years. At the beginning of succession, i.e., during facilitation, they can settle even better. From the adjacent areas, the more sensitive species, semi-natural vegetation, and even dominant grass species, cannot spread enough to prevent the settlement of other more sensitive species. This is because they have the best chance of getting into the basic matrix at the beginning [62]; thus, in the case of arable land and vineyards, the introduction and colonization of FS species in the studied period is continuous over time and there is no evidence of a large decrease in cover.

In the case of abandoned grasslands, the lack of mowing and grazing affects the equilibrium position, resulting in a decline in species that have adapted to mowing, as well as a reduction in diversity. On the other hand, species that do not like mowing or grazing, e.g., *Calamagrostis*, may multiply [45,46], especially if the equilibrium of the abandoned grassland is not stable. It is highly probable that, after abandonment, the two abandoned parcels of G/6–10 mentioned earlier had a different species set than the parcels of the previous age group, since *Brachypodium* was still not present after 6–10 years or had a low cover value. Other FS species achieved higher cover values in some places, but *Calamagrostis* and *Vicia cracca* typically dominated.

Based on our field experience, we hypothesize that *Brachypodium pinnatum* can replace *Calamagrostis epigeios* over a longer period of time (20–30–40 years) cf. [45,46]. The species pool of latter abandoned areas (1–5 and 6–10 years), which will expand in the next 20–30 years with species of more natural habitats (competitor and sensitive taxa), may also approach semi-natural grasslands with similar ecological conditions.

In a previous publication regarding the secondary succession of the area [31], it was explained that it was not the previous cultivation branches that determined the succession pathways, but rather the vegetation of the adjacent areas and the available species pool. Furthermore, in our field experience, exposure, soil moisture, and nutrient content also played a role in the regulation of succession processes [53].

However, in the second and third decades after abandonment, the absolute and relative cover of FS species significantly increased in the latter period, together with the increase in the number of species, and, in both periods, FS species accounted for the bulk of grassland production (Figures 2 and 3).

For all three abandoned types, both the absolute and relative cover of forest steppe species increased during the study period. Comparing the three types, abandoned grasslands had the highest absolute and relative total cover of FS species in each period. The absolute cover of FS species in abandoned vineyards and arable land similarly changed during the study period. Examining relative coverings in abandoned vineyards, the proportion of FS species was higher in the third decade after abandonment.

For the studied plots, the successional trajectories were determined by the dominance and competitiveness of at least two grass species: *Calamagrostis epigeios* and *Brachypodium pinnatum*. This was a result of field experience and cover values, in addition to the available propagule sources [31], based on the species-retaining and structure-stabilizing nature of *Brachypodium pinnatum* and the main properties of *Calamagrostis*, which slow down succession. In the case of abandoned vineyards, *Calamagrostis* appears in the first years after abandonment and begins spread strongly in most of the plots, reaching significant cover values in the first 5 years (average 40–50%). This significant cover value more visibly decreases for the oldest plots (average 22%). *Brachypodium* only appeared in the species group of the second age group; from then on, its average cover minimally increased over time. In the case of the oldest plots, where the *Calamagrostis* cover decreases, the matrix is formed of looser, more sensitive species, e.g., the spread of FS species becomes stronger, and they are able to create smaller patches cf. [31,62].

Contrary to the observations of others, e.g., [49,56], the segetal species did not form an independent succession phase in the abandoned fields of the study area in the first 5 years [31]. Two plots were dominated by *Elymus repens*, *Conyza canadensis* and *Erigeron annuus*, with *Calamagrostis* covering only one plot. In the second and third age groups, the cover of *Calamagrostis* significantly increased, becoming dominant, with *Fragaria viridis* reaching significant cover values. For the fourth age group, the mean cover value of *Calamagrostis* decreased compared to the previous two age groups. *Brachypodium* is present on a plot of the second and fourth age groups, respectively, with an increasing cover value. The reason for this is that, in the first years after abandonment, in addition to weeds, species of weed-like grasses and more natural grasslands also appeared. This can be explained by the more successful and faster colonization of taxa in neighboring areas due to the small size of the plots. In the case of some plots, the increasing dominance of the *Calamagrostis* also testifies to the role the adjacent areas play in determining the species composition. The early regeneration of the areas is indicated by the appearance of generalist and competitor species in the early years. As succession progresses, the proportion of forest steppe, as well as generalist, competitor and sensitive species also increases, confirming the rich propagule source of the landscape [31].

Of the abandoned areas, the most natural and the least variable are abandoned grasslands, which present the highest proportion of plant species in natural communities and the lowest share of weeds and non-native taxa. The former is also supported by the proportions of coenosystems, life forms, SBT and habitat categories. In the first age group, tall grass species that prefer mowing are still typical, and even dominant, in some places, e.g., *Arrhenatherum elatius*, *Dactylis glomerata*, *Anthoxanthum odoratum*. Of the FS species, *Brachypodium* does not represent a very high total coverage (13%), but can be found in all fallow areas. *Calamagrostis* occurred in two abandoned grasslands in one age group, where it was co- or sub-dominant, with a mean total coverage of 8%. The lack of mowing may have increased the expansion of *Calamagrostis epigeios* [46]. In addition to previous use, neighboring lands largely determine the dominant relations during secondary succession [31]. In the second age group, the average total cover of *Brachypodium* decreased compared to the previous group (6.5%), and one plot did not contain *Brachypodium pinnatum* at all. However, the average total cover of *Calamagrostis epigeios* increased to 13%. The latter was present in all three abandoned lands, and the fallow where *Brachypodium* was absent predominated in most of the samplings. *Brachypodium* is present in each of the two oldest age groups, with an average total coverage of 43–44%, while *Calamagrostis* was not present in any of the plots. Moreover, the high number and proportion of natural, sensitive and FS species should be emphasized, as this indicates the species-conserving nature of *Brachypodium* grasslands cf. [26,29].

One example of the dominant role of the vegetation environment can be found the oldest abandoned pastures and meadows, which are surrounded on almost all sides by abandoned grasslands, shrubs and tree patches. This means that their survival and naturalness are relatively assured [31].

4.3. Diversity

In the case of vineyards, the steady increase in diversity is consistent with the observations of Tatoni and Roche [63] and Debussche et al. [64] for some periods of abandonment. The slower increase in the diversity of FS species suggests that some of the species belonging to this group need time to ensure greater dispersal after successful recolonization. This can be influenced by the high abundance of *Calamagrostis*, which is considered a strong competitor [47,61] in 6–20-year-old vineyards. Nevertheless, the diversity could increase in the vineyards, even in the oldest studied age group.

In the case of arable land, the diversity values of FS species did not increase in all age groups, but showed an overall upward trend, similarly to other studies [47,49,65]. In line with the results of Tatoni and Roche [63] and Debussche et al. [64], the diversity of FS species showed a declining trend from the 20th year of abandonment. The small decrease in diversity observed with Age 4 is due to changes in the abundance values. Our results partially support the experience of Molnár and Botta-Dukát [66] and Monk [67], who showed that diversity did not linearly change during succession. The diversity of abandoned old-fields was influenced by the cover of species with strong competitive capacity [47,61].

In abandoned grasslands, diversity increased in two periods (age groups 2 and 4) but significantly decreased in between (age group 3), and so did not linearly change during succession, similar to Belsky's [68] experience. The significant decline in diversity in the second decade after abandonment is due to the fact that abundance values are more dispersed in this age group than in others.

In terms of Shannon diversity of FS species, grasslands were the most diverse in the first 5 years after abandonment, while the diversity of arables was the lowest (Figure 4). In the case of the oldest fallows, the order changed, since the average vineyard value was higher for the Shannon diversity, compared to previous pastures/meadows. When looking at abandoned lands with different cultivations, the initial (age group 1) diversity values were very different; however, after 30 years, these values became similar in a much narrower range.

4.4. Habitat Preference

In vineyards, the relative proportion of FS species steadily increased during secondary succession (Figure 5). In the oldest abandoned lands, their proportion was more than three times that of the youngest vineyards and, in the oldest fallows, over a third of the species were already FS species. The proportion of disturbed habitats has been steadily declining since abandonment; the proportion of the oldest age group is a third of that of the youngest. The proportion of steppe species more than tripled in the abandoned vineyards studied.

In abandoned arable land, the proportion of FS species more than doubled in the oldest wasteland compared to the youngest old-fields, while that of disturbed habitats steadily declined and fell to less than a quarter (Figure 5).

The proportion of the relative number of forest steppe species in the grasslands has doubled since abandonment and doubled compared to the youngest fallow land by the third decade, making up almost half (48.7%) of the abandoned pastures and meadows (Figure 5). The proportion of steppe species steadily increased in the first 20 years after abandonment.

In abandoned vineyards, the cover of forest steppe species increased the most after abandonment, but the cover of 'hay meadows, pasture, grassland' and steppe species also substantially increased, as did that of low-proportion mesophilous grassland species (Figure 6). In contrast, disturbed habitats and the cover of dry grasslands in the third decade were significantly reduced. These changes in proportions indicate a significant colonization of natural vegetation and a retreat by disturbing and dry grassland species by the third decade after abandonment.

Similar to abandoned vineyards, abandoned arable land shows a steady increase in the total cover of forest steppe species and a marginalization of 'disturbed habitats' species (Figure 6). As with vineyards, the 'dry grassland' species that were dominant since Age 2 also showed a significant share of the total cover. In addition, in the case of old-fields, the oldest age group showed the most balanced proportion of habitat categories in terms of cover. The fluctuating change in the relative cover of the 'steppe' and 'hay meadows, pasture, grassland' species in each age group is also striking, indicating the pulsating nature of vegetation dynamics in some habitat categories in abandoned arable land.

'Forest steppe' species proved to be the most-covered habitat category in the three of the four studied abandoned grassland age groups. The total cover of forest steppe species significantly increased following a decline fin their share between 6 and 10 years. By the third decade after abandonment, the cover of FS species accounted for more than three quarters of the cover of grassland stands. The relative cover of 'dry grasslands' and mesophilous grassland species steadily declined after abandonment. The relative cover of the former group and 'hay meadows, pasture, grassland' species, e.g., *Arrhenatherum elatius*, *Alopecurus pratensis*, which were used for mowing, decreased the most during the three studied decades. The decrease in the proportion of 'forest steppe' species observed at Age 2 coincides with the intermittent increase in the proportion of 'disturbed habitats' species that were only observed in this age group.

4.5. Coenosystematical Analysis

4.5.1. Coenosystematical Characteristics of Abandoned Lands

Following coenotaxonomic analysis of the examined age groups, the occurrence and proportion of four coenotaxones were found to be decisive in the texture of the abandoned lands: 1. indifferent species, 2. *Festuco-Brometea*, 3. *Festucetalia valesiaceae*, 4. *Quercetalis pubescentis-petraeae*. The species pool of *Brachypodium* grasslands derived from the latter three categories [26], and most of the forest steppe species in the Pannonicum Floristic Province occurred in these three coenotaxons; see [15]. The high cover of indifferent species may primarily indicate the age of abandonment, vegetation regeneration, and transient nature. The high proportion and number of indifferent species are characteristics of abandoned lands because they can be described as preferring multiple plant communities. In the initial and early stages of succession, plant communities with a stable, independent species pool and association-specific character species have not yet been developed. The indifferent species found in the studied abandoned areas have broad ecological tolerance, are disturbance-tolerant or, at best, are generalists cf. (Borhidi [42]). In terms of their life forms, these are less than 1–2-year-old weeds and are predominantly hemicryptophytes. The *Festuco-Brometea* (dry grasslands of South-Eastern Europe) class and its order *Festucetalia valesiaceae* (subcontinental dry grasslands), which is part of the forest-steppe formation [9], together with the order *Quercetalia pubescentis-petraea* (sub-Mediterranean and subcontinental xeroterm forests) show an increasing trend over time for all types of abandoned land. The latter coenogroups are mostly dominant in the oldest age groups, which supports the good colonization ability of the forest steppe species in the studied fallows, indicating that they spread from the refuge areas close to the plots.

The study area is characterized by natural or semi-natural species-rich grasslands, dominated by *Brachypodium pinnatum* [14,40], *Brometalia erecti* Order Br.-Bl. 1936 (sub-Mediterranean rocky, dry and semi-dry grasslands), and its *Cirsio pannonicae–Brachypodion pinnate* group did not appear as a result of coenotaxonomic analysis, although a wide range of order and group-specific species [9] can be observed in the older age groups. Furthermore, *Brachypodium pinnatum* grasslands are representative of semi-arid meadows, which are the most characteristic parts of the Pannonicum forest steppe complex in the Carpathian Basin [26].

The main habitat preference and coenotaxonomic categories roughly support each other's results, as the species of the dry grassland habitat type are mainly described in 5.3, 5.3.1. and 5.3.1.1 (*Festuco-Brometea*, *Festucetalia valesiaceae*, *Festucion valesiaceae*) and in the Indifferent coenotaxone (Table 1). Three-quarters of the habitat elements of the steppe belong to the coenotaxones 5.3, 5.3.1, 5.3.1.1, 5.5 (*Festuco-Brometea*, *Festucetalia valesiaceae*, *Festucion valesiaceae*, *Festuco-Puccinellietea*). The range of oak forest species was largely derived from syntaxons 8.4 and 8.4.2 (*Querco-Fagetea*, *Quercetalia pubescentis-petraea*). Most of the species affiliated with the meadow–pasture–hayfield habitat belong to the 5.4 *Molinio-Arrhenatheretea* and indifferent coeno-categories. Species classified as disturbed habitat are mainly listed in 3.3, 3.4, 3.5. (*Chenopodietea*, *Secalietea*, *Artemisietea*) and indifferent coenotaxones.

4.5.2. Coenosystematical Characteristics of Forest Steppe Species

In abandoned vineyards, the proportion of FS species classified in the *Festuco-Brometea* group steadily increased during secondary succession, but were not yet present in the first studied age group (Figure 7). In comparison, it is interesting that the elements of *Festucetalia valesiacae* FS have been present from the beginning, and their presence has changed little over the last 30 years. The latter syntaxa's species were included in equal proportions in the first and last of the studied age groups. The proportion of indifferent FS species showed a moderate decrease over time, while the proportion of FS elements in the *Quercetalia pubescentis-petraeae* group significantly decreased during secondary succession.

In abandoned arable land, *Festuco-Brometea* FS species appeared only in the second age group, where it was already co-dominant with *Festucetalia valesiacae and Quercetalia pubescentis-petraeae*. In contrast, *Festuco-Brometea* achieved only the second and third largest share in Age 3 and Age 4, so its proportion decreased over time. The FS elements classified in the *Festucetalia valesiacae* group also only appeared in the second age group, then their share almost stagnated. The proportion of co-dominant *Quercetalia pubescentis-petraeae* FS elements decreased over time, with less than half being found in Age 4 compared to Age 1. The proportion of indifferent FS species shows a declining trend during secondary succession. The latter dominate even in the oldest age groups.

In the case of abandoned grasslands, the FS elements of the *Festuco-Brometea* category are already present in the first age group, and even show dominance. They are also abundant or the most abundant in this type of abandonment over time, and their proportions are very similar in the youngest and oldest age groups. The FS elements of *Quercetalia pubescentis-petraeae* are already present in the first age group and are sub-dominant. Their proportion decreases for Age 3, but they represent the most abundant category in Age 4. The proportion of indifferent FS species was almost the same in the first and last age groups. In the second age group, their proportion almost doubled, resulting in their becoming the most abundant category. The proportion of *Festucetalia valesiacae* FS species showed minimal differences over the studied period.

Among the forest steppe species of abandoned vineyards, *Festuco-Brometea* elements were not yet present in Age 1, but their cover values show an increasing trend over time. They are already co-dominant or dominant in Age 2 and Age 3, while they are sub-dominant in Age 4. The abundance of forest steppe species belonging to the *Festucetalia valesiacae* group steadily increased during secondary succession and even dominated in Age 4. The share of forest steppe species classified in the *Quercetalia pubescentis-petraeae* group showed a sharp decreasing trend, followed by an increasing trend in the last age group. The mean total cover values of the indifferent FS species are not significant. It is interesting that their ratio was the highest (12%) in Age 4. The former phenomenon can be explained by the higher cover values of *Gallium mollugo* and *Inula salicina.*

In abandoned arable lands, the FS species of *Festuco-Brometea* and *Festucetalia valesiacae* appeared only in Age 2, with fluctuating cover values. *Festucetalia valesiacae* elements were dominant in Age 2 and sub-dominant in Age 4. FS elements classified as *Quercetalia pubescentis-petraeae* initially dominated, but their proportion sharply decreased in the oldest age group. Indifferent species were sub-dominant in the Age 2 group and dominated throughout the Age 3 and Age 4 age groups.

The total cover of forest steppe species in the *Festuco-Brometea* category only dominated in the age groups 3 and 4 (Figure 8), while *Festucetalia valesiacae* elements were dominant in the first and second age groups. The abundance of *Festucetalia valesiacae* FS species showed a decreasing trend. The cover of FS species in the group *Quercetalia pubescentis-petraeae* showed a fluctuating trend, but was sub-dominant in Age 2. The coverage values of indifferent FS species were not significant even at the beginning, and were barely present in the two oldest studied age groups. In the case of fallows and FS species, the main coenogroups were similar and the change in these categories showed a similar trend. Among FS species, the proportion of indifferent species was relatively high, which does not indicate a negative phenomenon in terms of vegetation dynamics regarding the naturalness of these species (see explanation in Section 4.5.1). Rather, the abundance of indifferent FS species indicates that FS species with a broader ecological tolerance that are not coenotaxonomically related to a particular association may be very successful at recolonization.

4.6. Multivariate Analysis

The hierarchical cluster analysis (Figure 9) reveals a successional trajectory for the FS species. For the two groups on the left edge, *Brachypodium pinnatum* is monodominant in terms of FS species' cover. For the detached 1–5 group of grassland on the right edge, along with the *Brachypodium pinnatum*, the *Festuca rupicola* is co-dominant. Towards to the core, the A/21–30 is dominated by the *Inula salicina*, the *Festuca rupicola* subdominates, and the *Brachypodium pinnatum* covers only 1% of the total.

In the groups between V/21–30 and A/1–5, the average total cover of *Brachypodium pinnatum* and *Festuca rupicola* decreases (between 0 and 6.8%), with other FS species becoming dominant or co-dominant and, less frequently, sub-dominant.

Thus, the formation of these groups was mainly based on the average total cover values of *Brachypodium pinnatum* and *Festuca rupicola* and, in more than half of the age groups, the values of other FS species also influenced the formation of the groups.

The age groups of the grasslands are well separated from the other groups—they are obviously the richest and most dominant in terms of FS species. Here, the former cultivation was decisive.

The age groups of arable lands and vineyards mainly alternate in chronological order: abandoned plots of a similar age are located next to each other, so the dominance of FS species is similar in terms of age group (Figure 9).

Finally, the resettling of arable lands and vineyards with FS species is basically derived from the time after abandonment and the vegetation of the adjacent plots.

This trend is consistent with the findings of Szirmai et al. [31], where the main regulatory factor for the primary succession of vineyards and arable lands was the vegetation of adjacent plots and the time after abandonment, instead of previous use.

4.7. Despite of Fragmentation

Forest steppe vegetation—for the previously mentioned reasons—is now typically found in a fragmented state in Hungary; however, they are particularly important due to—among other things—their role as a reservoir [62]. In the present research, we found 72 forest steppe species (out of 243 recorded species [31]) even in a relatively small area (only 4 km^2).

With the introduction of management, its changes, abandonment and time, the vegetation necessarily changes. In our 30-year chronosequence examination, we found that the number, proportion, cover and diversity of FS species increased, which further strengthens the importance of these habitats, despite their highly fragmented situation in the Pannonian Biogeographic Region.

5. Conclusions

Species number, absolute and relative cover, and the diversity of forest steppe species became significant for all three types in the oldest studied fallows. The latter is supported by the fact that FS species were dominant or sub-dominant, based on their cover. In the case of abandoned vineyards and arable land, the changes in the studied parameters of FS species had several similarities. In abandoned vineyards and arable land, the number and proportion of forest steppe species steadily increased, indicating the ability of forest steppe species to rapidly and efficiently recolonize, provided that an adequate supply of propagules is available around the abandoned areas. In addition, this is a good indicator of the efficient regeneration of vegetation for these habitats, as well as the direction of secondary succession in the studied hilly habitat. In abandoned vineyards and arable land, a further increase in the relative cover of forest steppe species can be predicted, even after the third decade of abandonment. In the case of abandoned grasslands, the increase in the number and cover of FS species indicates that the replacement of the species pool in these grasslands is not necessarily accompanied only by degradation, but also by the appearance and spread of valuable natural species, provided the abandoned plots are smaller and the habitat is sufficiently patchy. The overall average Shannon diversity of FS species became nearly identical in the third decade, despite the very wide-ranging characteristics of the initial period of abandonment.

In the case of abandoned vineyards and arable land, the equalization of the proportions of habitat categories can be observed as the abandonment progresses, while, in the case of abandoned pastures and meadows, the opposite trend can be seen. A common feature is that the cover rates of 'disturbed habitats' species were negligible for all three types in the third decade after abandonment, indicating a change in the quality of the species pool of abandoned grasslands. The secondary succession of abandoned lands can lead to the formation of semi-arid grasslands, especially where the fallows are already bordered by conventional semi-arid grasslands or dry oak forest patches, from which propagules of semi-arid grasslands containing many forest steppe species can spread.

Of the three studied types, in addition to the number of species and cover in abandoned vineyards, the diversity of FS species also continuously increased during the study period, indicating that FS species may play a key role in the recolonization of such habitats in the future.

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