



Cenopopulation of *Epipactis helleborine* (Orchidaceae) in forest ecosystems that have been anthropogenically transformed to various degrees

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Because of developed symbiotic connections of the root system of trees, mycorrhiza-forming fungi and the orchid family Orchidaceae in forest ecosystems of the northeast Polissia Region – cultivated *Pinus sylvestris*, which are now 100–120 years old, recovery of cenopopulations of *Epipactis helleborine* has been observed in locations of mixed and broad-leaved forests. In natural plant cover of mature pines of the region, indigenous vegetation is gradually recovering – there occur young *Quercus robur*, *Tilia cordata*, *Acer platanoides* of various ages, crown density of understory formed by *Coryllus avellana* has reached 0.6, above-ground organic leaf foliage that is able to sustain moisture and increase fertility of soil accumulates, creating sufficient conditions of shading for seedlings and juvenile individuals of forest orchids. Special studies revealed a relationship between density of *E. helleborine* specimens and crown density of the tree stand, shrub strata, structure of soil cover, expressed in cenoses under various degrees of recreational pressure. Density of individuals of forest orchids in the studied populations ranges 10.0 to 0.1 ind./10 m². Dynamics were seen in groupings of *Betuleto-Pineta corylosa*, *Querceto (roboris) corylosa*, *Querceto-Pineta corylosa*, *Acereto (platanoidis) –Tilieto (cordatae) – Quercetum (roboris) aegopodiosum* in the territory of the nature-reserve fund and structurally similar anthropogenically pressurized cenoses. We determined that all examined cenopopulations in old indigenous zonal cenoses in the territory of the nature reserve fund are normal, they may be considered relatively stable, ontogenetic spectra are incomplete, mostly with right-sided age spectrum – maximum numbers of virgin and generative individuals of various stages. Low density of individuals and incomplete spectra of cenopopulations in light oak forests are natural, and now the largest share of generative and virgin individuals is concentrated in this area. Impact of recreation, unavoidable due to proximity to a road, is a negative factor directly decreasing their density. Ontogenetic spectra of all cenopopulations are incomplete – no seedlings were found in the natural conditions due to underground type of germination. Much more interesting data may be obtained by monitoring studies of age and morphometric dynamic changes during several years.

Keywords: short-rooted forest orchids; late-successive biogeocenoses; locations of biodiversity; cenopopulation studies; ontogenetic structure.

Introduction

In Northeast Ukraine, the cultivated substitute of forest zonal cenosis-forming plants caused irreversible successions in the structure of typical indigenous cenoses – most species of the herb-shrub stratum, which are bioindicators, according to Braun-Blanquet (1964), diagnostic species of the largest class of forest vegetation *Querc-Fagetea* Br.-Bl. et Vlieger in Vlieger 1937 em. Klika 1939, represented by summer-green meso- and mesoxerophyte forests in mineral soils in the zone of moderate climate of geobotanical regions of Eastern Europe (Onyshchenko, 2009, 2017), specifically – the commonest species of forest orchids of *Epipactis* genus – *Epipactis helleborine*, became rare (Didukh, 2009).

The concept of complex study of rare species at the level of populations, based on the fact that any species lives in the wild as a separate local population (Zlobin, 2009), includes analysis of life forms, peculiarities of morphogenesis of individuals taking into account morphometric data, ontogenetic and vital structures of populations, reproductive specifics of plants, characteristics of ecotope and its correspondence to ecological needs of examined rare species. The status “rare species” and categorization of “rare species” (Stoyko, 2020) were used as basic criteria for choosing the object of monitoring studies. *Epipactis helleborine* is a polymorphic Palearctic Eurasian nemoral species with broad ecologic-nemoral amplitude. It has been introduced in North America and Canada, where it is considered a weed species (Light & MacConaill, 2006).

The objective of the study was performing complex comparative studies of cenopopulations of *E. helleborine* to determine life strategies of the species at population and organism levels, which manifest in the conditions of dynamics of anthropological pressure on protected and adjacent

territories in different types of successive broad-leaved forests in east Ukrainian Polissia. On lands that have been earlier occupied by indigenous forest ecosystems – mixed and broad-leaved forests, *Pinus sylvestris* trees are now 10–120 years old. Because of the developed symbiotic relationships between root systems of trees, mycorrhiza-forming fungi, species of herbaceous cover with obligate mycorrhiza, including the species we studied, the indigenous flora is recovering. Important components of the biocenosis are not only zonal dominants of tree stands of nemoral forests, understory, but also young *Quercus robur*, *Tilia cordata*, *Acer platanoides*, terrestrial fertile leaf foliage that is able to accumulate and restrain moisture, thereby increasing soil fertility. This creates sufficient conditions for shading seedlings and juvenile specimens of nemoral forest flora. We consider the discovered localities of *Epipactis helleborine* in Shostka geobotanical district separate cenopopulations, therefore we recognize their clear confinement to the surrounding conditions (Rabotnov, 1950; Zlobin, 2009).

The territory of the conducted studies is in the farthest northeast Polissia of Ukraine. It is a terrace lowland in the valley of the Desna River and the moraine-sandur plain – Yampil Plateau, segmented by river valleys of left-bank tributaries of the Desna–Svyha, Bychyha, Ivotka (tributaries – Kremliia, Ivot, Svisa, Studenok), Svirzha, Vita, Shostka (left tributary of the Ponurka), Osota, Esman (left tributaries of the rivers Hlystianka and Ret).

Forest in the region accounts for 28% of the area (Chornous, 2006), mean value for the Ukrainian Polissia being 29% (Andrienko et al., 2006). Indigenous tree stands of oak-pine and oak forests account for small areas in mostly nature-protected territories. In general, the region’s protected complexes of forest vegetation account for 192 km². In some forestries (Prudyschchianske, Olynske, Dubovytske, Zemliankivske, Sloutske, etc.),

over 300 year old oaks have preserved, indicating the former greatness of the region's forests. The network of objects of the nature-reserve fund in this territory is represented by 6 categories out of 11 existing in Ukraine. The percentage of protected area is 5.8. A total of 19 objects are located in the overall area of 9,480 ha, with only one forestry having State Protection status. Eight reserves are recognized as locally significant, as well as eight protected tracts. Climatic changes, aridization, against the background of global warming, gradual destruction of natural wetland, forest, meadow types of vegetation, disruption of hydrological regime of landscapes, increase in alien plants in the vegetative cover are some factors in the endless list of anthropogenic transformations. Not only are anthropogenic changes occurring in a particular nature region, but across the whole of Ukraine, and around the globe in general.

Materials and methods

According to the results of reconnaissance studies in forest tracts of the Shostka geobotanical district (Table 1) during 2003–2021, we found a large amount of newly discovered *E. helleborine*, which may suggest expansion of the species' range. The area we studied belongs to the European broad-leaved geobotanical region of the Eastern European (Sarmatian) province of coniferous-broad-leaved and broad-leaved forests of the Polisia coniferous-broad-leaved and Middle Russian subprovinces of leaved forests of Pryseimsky district of linden-oak, maple-linden-oak and oak forests, meadows and eutrophic wetlands (Didukh & Shelyah-Sosonko, 2003) within Ukraine. According to physical-geographic zoning, it is a zone of mixed forests of Eastern-European physical-geographic province (Marinich et al., 1968).

As model object, we chose *E. helleborine*. Sample plots were established in forest blocks with the most numerous populations of the species. In sample plots, on both sides of 146 to 400 m long transects along the glade and from the node in the direction deep into the forest, we established 1 x 1 m squares. In each square, on the spot, we identified and counted plants of various age groups. High frequency of the species' occurrence in plots of geobotanical descriptions allowed us to obtain reliable selection. Studying and describing ontogenesis in field conditions is practically impossible due to peculiarities of biology (presence of protocorm and mycorrhizae, which have been in forest litter for 9 years). Vegetative reproduction was observed in less than in 5% of individuals, took place by division and dying of old regions of root systems during formation of two and more above-ground shoots, leading to particulation. By type of reproductive strategy, it belongs to species with stable dominance of seed reproduction.

A counting unit was considered a partial individual with a single-axis separate individual shoot of *E. helleborine*, regardless of whether it was a genet or ramet. The counting unit (specimen) is a complex individual with long existing geophilic areas of shoots as residuals of the root system. Short-rooted species and borders of individuals in natural conditions were impossible to determine, since we used only undamaging methods of morphometry in the territory of the nature-reserve fund where rare species included in the Red Book of Ukraine grow (Didukh, 2009). Forest litter was not dug in order to avoid damaging the populations and no plants were dug out of it. Specifics of the biology were analyzed according to a number of studies (Varlygina & Vakhromeeva, 1998; Efimov, 2004; Vakhromeeva et al., 2014). *Epipactis helleborine* is a herbaceous polycarpic plant with perennial sympodially overgrowing monocyclic vegetative-generative skeletal long-shoot axes. It is geophyte or axillary-rooted hemi-cryptophyte, the roots live for over 3 years, hypogenically-short-rooted with short stem parts of stem-root tuberosities, short internodes of monopodially overgrowing shoots, with no specialized accumulating organs. Axillary roots are located on typical roots. Shoots have no thickenings. Summer-green plant with 30–100 cm long above-ground shoot and 3–5 months life span of leaves.

Three groups of leaves were seen in *E. helleborine* (Serebrjakov, 1952):

1) lower formations: type I – scale-like leaves of roots; type II – transitional leaf (cataphyll) in the restoration zone; type III – sheath leaf with underdeveloped leaf lamina;

2) middle formations: type I – transitional sheath leaf with insufficiently developed leaf lamina with rounded apex; type II – well developed

sheath leaves with sharpened apices; type III – small sessile leaves, transitional to bracts;

3) upper formations – bracts of inflorescences.

Since the life cycle of *E. helleborine* lasts for 30–35 years, it is very hard for one scientist to study its ontogenesis. Measuring and distinguishing ontogenetic conditions were carried out according to the concept of discrete description of ontogenesis (Light & MacConaill, 1994).

Seeds (sm) – productivity – 3–4th in fruit, one individual can form around 26 th seeds. Actual seed productivity of adult generative individuals was not determined. Research shows that after entering the soil, it remains latent for 9–12 months, and only 5% germinate after fungal infection, and therefore reproductive success is low. The determining limiting factor of seed germination, and therefore tolerance of populations, is formation of mycorrhiza with the same fungi as the dominant species of trees. Intensity of mycorrhiza formation to a high degree depends on fertility and moistening of the substrate (Perebora, 2011).

Seedling (p) lives underground. It comprises protocorm and mycorrhizome. Protocorm is initial stage of post-seed development of sporophyte of orchids before bud formation. The mycorrhizome is the initial shoot with scale-like leaf. We found no seedlings.

Juveniles (j) – plants starting from year 9, since appearance of first leaf on first above-ground shoot, after transition to autotrophic nutrition. The shoot has 1–2 types I and II middle formation leaves. Leaf length is 5–6 cm, width is 1.0–1.5 cm. Internodes are short.

Immature (im) plants bear 3–4 type II leaves of middle formation, 6–8 cm long and up to 3 cm wide, with shortened internodes.

Primarily virgin (v), or adult vegetative plants have 4–5 type II leaves of middle formation, 7–11 cm long and 2–4 cm wide. Internodes are shortened, and there is false whorl at the apex.

Annually blossoming for many years *E. helleborine* transits into second latent condition for 2–7 years or only vegetates for several years, because inflorescences of species of *Epipactis* and *Cephalanthera* genera are developing inside buds for 13–14 months. Plants have external morphological features: dried apex with clearly expressed external features of dying; axis of inflorescence is well-developed, has no generative organs, there is 1 – rarely 2 – type III sessile leaves of middle formation on the axis.

Secondary virgin (vv) – we determined that the average height of such individuals is 30 cm. Plants have a large transitional type I leaf of middle formation, 5 and more type II leaves of middle formation, 7–11 cm long, 2–4 cm wide. Internodes are elongated. False whorl is absent. Number of leaves is always 1–2, type III middle formation.

Generative (g) – they blossom for the first time in 10–11th year, have 4–6 (8) leaves, 7–12 cm long, 3–6 cm wide.

As marker diagnostic features of generative conditions (g₁, g₂, g₃), we used: length of shoot, number of stem leaves (middle formation), number of veins in leaf lamina, extent of manifestation of internodes (long, short), length of the first internode of inflorescence, number of flowers in it.

Young generative (g₁) – first 10 years of blossoming – plant in the 20th year of its life. Leaves: 1 type I large transitional leaf of middle formation, 4–5 – type II, 1 – type III. In inflorescence, the number of flowers is low, the first internode is short.

Average-generative (g₂) – second decade of blossoming. Plants have large type I transitional leaf of middle formation, 6–8 type II and 1–2 type III leaves. First internode is very short. Inflorescences are loose raceme, long, with lots of flowers.

Old generative (g₃) – third decade of blossoming. Type I leaf of middle formation – 1 small, 3–4 type II and 1 type III leaves. The first internode of inflorescence is short, with low number of flowers.

Senile (s) plants are old vegetative plants with 6–7 leaves, with no generative shoot, fruit-bearing stops. In the wild, ontogenetic condition is seen rarely, because many plants die right after they blossom for the last time.

To determine the degree of the development of generative individuals using methods of non-destructive morphometric technique, we took into account 7 features: H_{veg} – overall length (height) of vegetative shoot (cm); H_{gen} – general length (height) of generative shoot (cm); N_{fil} – number of developed shoot leaves (quantity); L_{fil} – leaf length (cm); L_s – leaf width (cm); n – number of veins, L_m – length (height) of inflorescence (cm); N_{fl} – number of flowers in inflorescence (quantity).

Table 1
Forest tracts of the Shostka Geobotanical District

Name of river (tributary), in terraces of which forests grow	Names of forest tracts	Geographic coordinates of forest center			Outskirts, cities
		latitude	longitude	altitude, m	
Right bank of the Svyha River (Desna)	Shvaikivshyna	52.1892	33.7370	176	North of Hutko-Ozhynka village
Right bank of the Svyha River (Desna)	Myhailivshyna	52.1883	33.7034	167	Northwest of Hutko-Ozhynka village
Right bank of the Svyha River (Desna)	Yasna Haliavyna	52.1894	33.7477	166	North of Krasychka village
Right bank of the Svyha River (Desna)	Dubolissia	52.2052	33.8084	169	North of Lukashenkove village
Headwaters of the Esman (Kleven)	Vedmezha Ravine	51.7528	33.7864	181	South of Bereza village
Floodplain of the Esman	Pliushcheva Ravine	51.6955	33.3444	155	Between Slout and Chervone villages
Headwaters of the Esman (Kleven)	Orliv Gully	51.7143	33.8636	174	Between Pervomaiske, Pustohorod, Horile villages
Right bank of the Esman River	Turovi Poliany glades	51.7551	33.7261	201	West of Slout village
Left bank of the Esman River	Brod	51.7438	33.7588	186	Southwest of Slout village
Right of the Esman River	Shchyhalnytsia	51.7645	33.6047	195	North between Kudriumivka and Huta villages
Headwaters of the Muraveinia River	Borok	51.7572	33.6369	197	Northeast of the Huta khutir
Area between the Esman and the Shostka rivers	Volkovo	51.7664	33.5926	189	Between Hukovo and Huta khutirs
Headwaters of the Hlystianka (Esman)	Prybludino	51.6619	33.4358	161	Around Bilohryve village
Flood plain of the Ret River	Kravchenkova mountain	51.6328	33.5858	162	Northeast of Dubovychi village
Right bank of the Osota River	Velyke Boloto wetlands	51.7834	33.2522	135	Northwest of Klyshky village
Right bank of the Esman River	Kolodsi	51.7361	33.5275	164	Between Peremoha and Kushkino khutirs and Zemlianka village
Right bank of the Esman River	Tyvoniv gully	51.7253	33.6604	192	Northeast of Shevchenkove village
Flood plain of the Rokyta (Esman)	Nechaievshchyna	51.6566	33.4580	168	West of Oblozhky village
Right bank of the Ret River	Hruzke	51.6027	33.4436	152	East of Hruzke village
Right bank of the Osota River	Viunishche	51.7262	33.4105	155	Northwest of Voronizh
Left bank of the Osota river	Voronizke	51.7511	33.4017	172	South of Masykiv village, west of Voronizh
Floodplain of the Ivotka River	Lomlenka	51.9998	34.1210	186	North of Lomlenka village
Left bank of the Ivotka River	Velyka Voloka	51.9052	33.5619	160	North of Myronivka village
Headwaters of the Sheinka (Ivotka) River	Nepliuivshyna	51.9665	34.0406	174	West of Marchyhyna Buda village
Area between the Ivotka and the Svesa rivers	Kryvi Richky	51.9442	33.9335	159	North of Svesa town
Left bank of the Kremlia River (Ivotka)	Rudnia	51.9804	33.8500	143	Outskirts of Yampil, near Nepliuieve village
Right bank of the Ivotka River, between the Kremlia and the Ivotka rivers	Kremlianska Dachka	51.9766	33.8480	156	Around Chyzykovo khutir and Nepliuieve village, north of Yampil
Left bank of the Svesa River	Pastba	51.9477	33.7866	165	West of Orlivka and east of Yampil
Left bank of the Sheinka River	Demianivske	51.9566	34.1316	185	East of Demianivka khutir
Headwaters of the Usok River	Krynichky	51.9041	33.7769	178	Southwest of Imshana village
Right bank of the Ivotka	Novopokrovske	52.0080	33.7580	161	North of Belytsi and Derazhnia villages
Right bank of the Ivotka	Hresty	52.0421	34.0297	170	East of Chuikivka village
Headwaters of the Usok rivers	Dovha Loza	51.9840	33.6073	163	Outskirts of Usok village
Right bank of the Ivotka River	Khutoryshche	51.9829	33.5460	148	Between Antonivka and Ivot villages
Right bank of the Ivotka River	Radkib Bir coniferous forest	51.9592	33.4449	145	Between Pohrebky and Ivot villages
Headwaters of the Laronivka River	Sytnykyv Klyn	52.0241	33.6819	157	Between Shatryshche and Antonivka villages
Headwaters of the Laronivka River, right bank of the Ivotka River	Dibrovne	52.0036	33.5869	169	North and northwest of Antonivka village
Right bank of the Ivotka River	Khutoryshche	51.9921	33.5460	144	Between Antonivka and Ivot villages
Right bank of the Usok River, between the Usok and the Ivotka rivers	Puryziv Zrub	51.9305	33.6696	160	North of Palievka, Usok, Olhyno villages
Between Ivotka and the Shostka rivers	Kirovska Dachka	51.9071	33.4125	147	Between Obrazheivka and Myronivka villages
Floodplain of the Svyha River (Bychyha)	Dubova Koma	52.1272	33.9908	173	Between Kamianka, Shalymivka and Sytne villages
Floodplain of the Shostka River (Ponurka, Liuta)	Shakutivshchyna	51.8111	33.8730	190	Between Horily and Shakutivshchyna khutirs
Headwaters of the Esman (Kleven)	Kryvenkove	51.8038	33.8424	180	Between Kryvenkove village north of Ivashchenkove village
Right bank of the Shostka River	Bukatovshchyna	51.8340	33.6245	190	Between Makove and Turanivka villages
Right bank of the Ponurka River	Turovshchyna	51.8297	33.7891	174	North of Dolyna village
Right bank of the Shostka River	Krynichky	51.8427	33.7733	181	West of Turanivka village
Right bank of the Shostka River	Miliutyn Forest	51.8867	33.3759	133	Between Lazarivka, Obrazheivka, Bohdanka villages
Left bank of the Shostka River	Ushynske	51.8622	33.3643	136	South of Bohdanka village
Right bank of the Shostka River	Myhailivska Dachka	51.1122	33.3722	163	North of Makove and Hamaliivka villages
Headwaters of the Usok River, area between the Shostka and the Ivotka rivers	Dovha Loza	51.9154	33.6422	177	South of Palievka and Usok villages
Left bank of the Desna (Dnipro) river, area between the Shostka and the Osota rivers	Hlyboky Kolodiaz	51.8086	33.1327	140	Between Tymanivka and Sobykh villages
Left bank of the Desna (Dnipro) river, area between the Shostka and the Osota rivers	Velyky Bir coniferous forest	51.8095	33.1759	156	Between Tymanivka and Sobykh villages
Left bank of the Desna (Dnipro) river	Kirovska Dachka	51.9052	33.5619	160	West of Myronivka village

Categories of the populations were determined according to the generally adopted methods (Uranov, 1975, 1977; Smimova et al., 1976; Zlobin, 2009). The conditions were evaluated according to types of age spectra, their completeness, number, density per unit of examined area. We analyzed the conditions of the populations depending on age of the tree stands. The populations were described according to different extents

of recreational pressure in the territories of the nature reserve fund – in nature reserves, in conditionally primary (100 years) forest ecosystems under moderate recreational pressure, under strong recreational pressure, late-succession (100–120 years).

Our own data of geobotanical descriptions are materials for determining ecological-cenotic peculiarities of forest ecosystems. Geobotanical descrip-

tions were analyzed, syntaxa were distinguished and identified according to “Prodromus of vegetation in Ukraine” (Dubyna et al., 2019) and “Green Book of Ukraine” (Shelyah-Sosonko & Andrienko, 1987; Shelyah-Sosonko et al., 2002; Didukh, 2009) in the dominant system of classification; in the floristic system – according to methods of Braun-Blanquet (1964) and Onyshchenko (2009, 2017). A total of 6 populations were studied (Table 2) in different associations: conditionally primary – oak-pine forests with hazel, birch-pine, oak-hazel, light oak forests, maple-linden forests with elder oak forests, aspen-birch-pine forests of alder buckthorn-grass (light oak forests) and disturbed forests (birch-pine hazel forests).

Table 2

Ecological-cenotic characteristics of forest ecosystems in sample plots within the Eastern Left-Bank Polisia of Ukraine, 2021

Administrative location, protection category	Group according to dominant/floristic classification	Age of tree stand, years	Density of tree crowns	Density of understorey crowns	Projective cover of grass stand, %	Density, ind/10m ²
Verhniomansky Reserve, Sloutske Forestry, Turovi Poliany, block 77	Querceto-Pineta coryllosa/Corylo avellanae-Pinetum	60–70	0.8	0.7	40	3.3
Verhniomansky Reserve, Zemliankivske Forestry, Hutianske (Kolodtsi) Tract, block 22, compartment 14.1	Betuleto-Pineta coryllosa/Carici pilosae-Quercetum roboris	90–110	0.7	0.8	40	10.0
Dubovytskr Forestry, block 53, 65	Querceta (roboris) coryllosa/Carici pilosae Quercetum	100–120	0.8	0.7	25–30	6.5
Protected Tract Pidivotsko-Chuikivska Dacha. Chuikivske Forestry, block 32, compartment 18	Quercetum convallariosum, Quercetum pteridiosum/Lathyro-Quercetum	100	0.6	0.1	60–70	0.4
Reserve Ushynsky, Shostkynske Forestry, block 33, compartment 6	Acereto (platanoidis)–Tilieto (cordatae)–Quercetum (roboris) aegopodiosum	90–100	0.8	0.6	50–60	1.4
Olynske Forestry, block 43, compartment 1	Populeto–Querceto–Pineta coryllosa/Carici pilosae Quercetum	80–90	0.8	0.5	10	0.1

Table 3

Results of morphometry of morphological features of leaves of middle formation of *Epipactis helleborine*

Ontogenesis condition	Leaves of the middle formation								
	Type I			Type II			Type III		
	N _{fl.} quantity.	L _{fl.} cm	L _{so.} cm	N _{fl.} quantity.	L _{fl.} cm	L _{so.} cm	N _{fl.} quantity	L _{fl.} cm	L _{so.} cm
j	0	0.0	0.0	1–2	5.5	1.2	0	0	0
im	1	1.6	0.7	3–	6.30	1.8	0	0	0
v	1	2.7	0.8	4–5	9.0	3.0	0	0	0
vv	1	2.3	1.3	4–5	9.0	3.0	1–4	1.2	0.2
g ₁	1	3.5	0.6	4–5	7.0	4.0	1	2.2	0.5
g ₂	1	6.8	0.7	6–7	10.6	6.0	1–2	2.3	0.9
g ₃	1	3.8	0.6	5–6	12.5	6.5	1	2.2	0.9
s	0	0.0	0.0	6–7	10.0	5.0	0	0	0

Table 4

Results of morphometry of morphological features of leaves of upper formation and internodes of *Epipactis helleborine*

Ontogenesis condition	H _{veg.} cm	Internodes										
		Formation of leaves apex (involucrum)			vegetative shoot			false whorl			inflorescence	
		N _{fl.} quantity	L _{fl.} cm	L _{so.} cm	shortened	elongated	present	absent	short	elongated		
j	8.0	–	–	–	shortened	–	–	absent	–	–		
im	14.0	–	–	–	shortened	–	present	–	–	–		
v	17.0	–	–	–	shortened	–	present	–	–	–		
vv	30.5	2–4	2.5	0.5	–	elongated	–	absent	–	–		
g ₁	25.5	13	2.3	1.2	–	elongated	–	absent	short	–		
g ₂	55.0	33	2.2	0.5	–	elongated	–	absent	–	elongated		
g ₃	32.5	6	2.4	0.9	–	elongated	–	absent	short	–		

Note: “–” absence of the indicated morphological features in leaves of apex formation (involucrum) and internodes.

Table 5

Ontogenetic spectra of cenopopulations of in succession forests in the territory of Shostka geobotanical district

Population	Number of specimens per 1,000 m ²	Proportion of age groups, %						
		j	im	v	g ₁	g ₂	g ₃	s
1	227	1.2	11.0	48.1	6.1	17.4	7.3	8.9
2	250	4.9	15.2	21.5	4.0	35.7	14.5	4.2
3	180	5.2	9.2	25.3	5.3	34.2	12.7	8.1
4	37	0.0	8.9	22.2	37.8	22.2	0.0	8.9
5	145	10.9	16.7	31.6	3.4	19.6	8.0	9.8
6	17	0.0	0.0	11.8	0.0	88.2	0.0	0.0

Cenopopulation 1 of E. helleborine. Successional forest. Multi-storey groups of *Querceto-Pineta coryllosa/Corylo avellanae-Pinetum*. Composition of tree stand 9J1W-8J2W. Crown density equaled 0.6–0.7. In stratum I – *Pinus sylvestris*, 20–30 m high, trunk diameter equaled 24–46 cm, II–III bonitet (productivity class). In stratum II – *Quercus robur*, 16–18 m high, with 24–46 cm trunk diameter, II–III bonitet. There occur young

Results

According to the results of morphometry, we obtained materials for distinguishing g₁, g₂, g₃ conditions of generative age period of ontogenesis. Additional diagnostic features for identification: quantity, sizes of leaves of middle and upper formations, length of internodes, presence/absence of false whorls of leaves, number of involucra of inflorescence, distance between the nodes of involucra (Tables 3, 4). The results of morphometry are given in Tables 4, 5. Leaves of lower formation are not described, as we had not dug the soil and forest litter.

plants of *Q. robur*, *Betula pendula*, *Acer platanoides*, *Tilia cordata*, *Ulmus laevis*, *Pinus sylvestris*, *Picea abies*, *Sorbus aucuparia*, *Pyrus communis*. In the understorey stratum (0.4–0.7), *Corylus avellana* dominates, and *Frangula alnus*, *Sambucus racemosa*, *Sorbus aucuparia*, *Rubus idaeus*, *R. nessesensis*, *Padus avium*, *Acer negundo*, *Amorpha fruticosa* occur. The floristic “kernel” of the herbaceous-shrub layer is mainly

represented by nemoral species, the number of species on average per one geobotanical description (400 m²) equaled 29–30, projective cover was 40–85%, dominant plants were *Stellaria holostea* (20–30%), subdominants were *Carex pilosa*, *Pulmonaria obscura*, *Glechoma hirsuta*, *Lathyrus vernus*, *Trientalis europaea*. This cenosis is included in the first and second editions of The Green Book of Ukraine: Syntaxon 11. The group of associations of oak-pine forests with hazel *Querceto-Pineta corylosa* is a typical old indigenous forests of the Polisia, where *E. heleborine*, *Neottia nidus-avis*, *Primula veris*, *Lilium martagon* grow in floristically-rich sites. In the studied region, rare cenoses of such type have been described and are protected in Bohdanivsky and Voronizky Reserves (Ass. *Querceto-Pinetum* Cl. *Querceto-Fagetea*). Total number of this population is almost impossible to determine, because it potentially may be over 1,000 specimens per general area of compartment or block. Therefore, we should consider the average density. At the distance of 10 m from the node, average density was the highest – 3.3 ind./10 m². In 100 x 10 m area along the transect, we observed more than 227 plants of *E. helleborine*. The population was young. Age spectrum was normal, incomplete, left-sided monomodal with virgin specimens accounting for the maximum number of individuals in the share (48.1%). The generalized data of completeness of ontogenetic ranges in different types of successive cenoses are presented in Table 6.

Cenopopulation 2 of E. helleborine. Late-successional forest. It is an area of birch-pine forest with hazel *Betuleto-Pineta corylosa* (*Carici pilosae* – *Quercetum roboris* (*Mercurialo-Quercetum*, *Aceri campestris* – *Tilietum cordatae*)) aged 90–110 years, which comprises *Pinus sylvestris*, where leaved species are undergoing recovery. Tree stand 5J5D, 8J2D: *Pinus sylvestris* of 30–32 m height, with 38–42 cm diameter. *Betula pendula* was 24–26 m high, 22 cm in diameter, and crown density equaled 0.7–0.8. The understorey (0.6–0.8) was composed of *Corylus avellana*. The floristic “kernel” of herbaceous-shrub stratum was represented by *Aegopodium podagraria*, *Carex pilosa*. This cenosis is included in the first and second editions of Green Book of Ukraine: Syntaxon 11. Group of associations of oak-pine forests with hazel – *Querceto-Pineta corylosa* – typical old indigenous forests in Polissia. In the region, cenoses are protected in the territory of Dibrova and Kniazhytsky Landscape Reserves of local significance and Pidivotsko-Chuhuivska Dacha and Dialianka Lisu Botanical Reserves. In the area of 250 x 4 m, the number exceeded 250 individuals with maximum density of 10.0 ind./10 m². The plants grow separately, more rarely in groups of 3–4 individuals in each. Incomplete (no seedlings and senile plants), normal, is characterized by right-sided age spectrum peaking at middle-generative. Share of temporary non-blossoming generative individuals, which after g₂ g₃ period transit into virgin ontogenetic condition, accounts for 5%.

Cenopopulation 3 of E. helleborine. Conditionally ancient forest, typical groups of old ancient oak forests. According to Green Book of Ukraine, it is syntaxon 32. Group of associations of forest with hazel – *Querceta (roboris) corylosa*, with dominance of nemoral, broad-leaved, broad-range and boreal species. The tree stand is 10W+J+D, crown density was 0.6–0.7. *Quercus robur* was aged 80–90 years and was 28–30 m high, 38–40 cm in diameter. There were singular young plants of various size, namely *Acer platanoides*, *Tilia cordata*. The understorey’s density is 0.5–0.6, 6 m high; dominating species in richer edaphic conditions is *Corylus avellana*, and single plants of *Frangula alnus*, *Euonymus verrucosa*, *Sorbus aucuparia*, *Rubus idaeus* occur. Herbaceous stand is uniform (60–70%). In floristically rich groups of old areas of *Querceta (roboris) corylosa*, apart from *E. heleborine*, there were *Neottia nidus-avis*, *Primula veris*, *Digitalis grandiflora*. In the region, there are the Verhnoiesmanskyy, Velyky Bir, Bir Masyyv, Dibrova, Voronizka Dacha, Pirotchynska Dacha, Bilohryve, Tipka, Dilianka Lisu reserves. In the area of 200 x 6 m, there were recorded 180 individuals. The population is normal, incomplete, age spectrum is right-sided, single-modal, with peak at middle-generative individuals (50.6%). It is a mature population, transitional to aging.

Cenopopulation 4 of E. helleborine. Conditionally ancient forest, area of sun-lit floristically rich group of associations of *Quercetum convallariosum*, *Q. pteridiosum*, *Populeto-Quercetum franguloso graminosum*. Areas are characterized by high floristic diversity, absence of expressed dominants in the lower strata, on average 69 species of higher vascular species per one geobotanical description, or 50–55 species per 100 m².

Tree stand (0.6) is 18–20 m high, over 70–80 years old, formed by young shoots of *Q. robur*. Also, there occur *Populus tremula*, *B. pendula*, *Tilia cordata*, *Acer platanoides*. Sparse understorey is composed of *Frangula alnus*, *Sorbus aucuparia*, *Berberis vulgaris*, *Euonymus verrucosa*. There are many young plants of *A. platanoides*, *Q. robur*. Cover of herbaceous-shrub stratum is 70%. The following rare and uncommon species were found: *Lilium martagon*, *Epipactis heleborine*, *Platanthera bifolia*, *Peucedanum cervaria*, *Campanula cervicaria*, *Aster amellus*, *Digitalis grandiflora*, *Iris hungarica*, *Laserpitium prutenicum*, *Genista germanica*, *Serratula tinctoria*, *Thalictrum aquilegifolium*, *Primula veris*, *Dianthus stenocalyx*. According to modern schemes of ecological-floristic classification, the groups belongs to Ass *Lathyro nigri-Quercetum roboris* Bulokhov et Solomeshch 2003 Cl *Quercetea pubescenti-petraeae* Jakucs (1960) 1961 and are close to the Central-European association of *Potentillo albae-Quercetum petraeae* Libb. 1933 group of *Quercion petraeae*, in the herbaceous stratum of which, meadow-steppe and glade species dominate Cl. *Querceto-Fagetea* Br.-Bl. et Vlieger 1937, described from southern parts of Polisia of Poland and Ukraine. In the studied region, it is protected in the Prudshchansky (block 53) and Kremliansky (block 58) forestries of Yampil district, Verhnoiesmanskyy reserve. The population in the area of 200 x 6 m is characterized by low density equaling 0.37 ind./10 m². The population is normal, incomplete, single-modal, mature, with right-sided spectrum with significant share of generative plants (60%), with g₁ dominating.

Cenopopulation 5 of E. helleborine. Conditionally ancient forest. The forest is a valuable site of old broad-leaved forests, included in The Green Book of Ukraine: syntaxon 37. Association of maple-linden-oak forests – *Acereto (platanoidis) – Tilieto (cordatae) – Quercetum (roboris) aegopodiosum*. *Acereto-Tilieto-Quercetum caricosum (pilosae)*. In the Eunis system: W1.2.2 East-European mesophilous eutrophic forests of common oak and small-leaved lime of the forest zone. Syntaxonomic composition: *Acereto (platanoidis) – Tilieto (cordatae)-Quercetum (roboris) aegopodiosum*, *Acereto (platanoidis) – Tilieto (cordatae)-Quercetum (roboris) caricosum (pilosae)*, *Mixeto-Quercetum alliosum (ursini)*. Cl *Querceto-Fagetea*. This population includes *Populeta tremulae*, represented by associations of *Populeto (tremulae) – coryloso (avellani) caricoso (pilosae)*. Height of the tree stand is 16–18 m, crown density is 0.8–0.9; other than the dominant species, *Quercus robur* and *Tilia cordata* occur. The understorey is 0.4, 5–6 m high, formed by *Corylus avellana* (0.4), singularly – *Euonymus verrucosa*, and young plants of *Tilia cordata*. Herbaceous cover is 60%, with dominant *Carex pilosa* accounting for 30%. In the region, it is also protected in the Bohdanivsky Reserve, Turvshchyna and Krynychky forest tracts. In the area of 200 x 6 m, we observed over 45 specimens. Normal (definitive) incomplete, one-modal, left-sided, with peak at virgin individuals. The population is aging, since the majority of virgin individuals are temporarily non-blossoming specimens.

Cenopopulation 6 of E. helleborine. Successional forest. A highway has been paved across the forest. The described plot is on a roadside and is generally spread across the oak-pine forest (*Populeto-Querceto-Pineta corylosa/Carici pilosae-Quercetum*) with scattered *Populus tremula*, *Betula pendula*, *Picea abies*. The understorey is composed of *Corylus avellana*, with 0.6 density. Terrestrial cover is almost without mosses, the structure of the cenosis has been disturbed by presence of synanthropic species. Young plants are *Acer platanoides*, *Tilia cordata*. Among natural nemoral species, there are *Aegopodium podagraria*, *Stellaria holostea*, *Asarum europaeum*. This population is the smallest by spread area (400 m²), number (17 individuals) and density (0.1 ind./10 m²). The ontogenetic spectrum is incomplete – we saw no rejuvenation – there are no juvenile and immature plants, indicating instability, right-sided, – we only found virgin and generative individuals, which dominated.

Discussion

Harmful forestry practices had caused destructive impact on the composition and structure of typical primary cenoses that have become rare. At the same time, cenotic vulnerability is related to floristic. Many species of forest orchids are rare not only in Ukraine (Timchenko, 1996; Efimov, 2004; Prots, 2010; Lubka, 2018; Fateryya, 2018a; Calevo & Bazzicalupo, 2020; Efimov, 2020; Khapugin, 2020; Popovich et al., 2020; Kirillova &

Kirillov, 2021). Species of *Epipactis* genus are characterized by vulnerability in Central Europe (Melnik, 1996; Molnár & Sramkó, 2012; Djordjević, 2016), Caucasus (Perebora, 2011; Fateryga et al., 2018b), Russia (Efomov, 2004; Vakhrameeva et al., 1997, 2014; Seregin, 2018), United States, Canada, North Africa, Middle East (Delforge, 2006).

Old *Quercus robur*, *Tilia cordata*, *Acer platanoides* are essential for preservation of mycorrhiza tree associations, long term hypogean survival of orchids (Light & MacConaill, 2006). This reflects significance of indigenous forests. Our data about floristic discoveries of *E. helleborine* in the territory of Shostka geobotanical district (Chomous & Andriyenko, 2004; Chomous, 2005, 2006) are specifically related to old cenoses. The recent reports (Panchenko & Ivanec, 2019) indicate increase in well-known localities.

Around 100 years ago, before intensive forestry was introduced in the northeast Ukraine, most forested areas of the region were broad-leaved associations of *As. Mercurialo perennis-Quercetum roboris* Bulokhov et Solomeshch 2003 group *Quercus roboris-Tilia cordatae* Solomeshch et Laivins 1993 ex Bulokhov et Solomeshch 2003, with light oak forests of *As. Lathyro-Quercetum* of class *Quercetea pubescenti-petraeae* Jakucs (1960) 1961 (Panchenko & Onishchenko, 2005; Panchenko, 2018). We saw such examples in a number of objects of the nature-reserve fund (Prudyschansky Regional Landscape Park, Verhniomiansky, Velyky Bir, Dibrova Reserves, etc.) at the locations of primary cenoses, which at the age of 60, at the stage of restorative successions, have formed *As. Corylo avellanae-Pinetum sylvestris* Bulokhov et Solomeshch 2003 (group *Quercus-Tilion*) and *As. Quercus-Piceetum* (W. Matuszkiewicz 1952) W. Matuszkiewicz et Polak 1955 (group *Melico nutanstitis-Piceion abietis* (Killand-Lund 1981) Onyshchenko 2005 prov.). At such plots, the dominant species in the tree stand is *Pinus sylvestris*, and cenotypic positions of *Quercus robur* are being gradually recovered, and under the crown of *Corylus avellana*, young individuals of species of shaded broad-leaved forests grow with *Acer platanoides*, *Tilia cordata*. The “kernel” of the herbaceous-shrub stratum is formed by nemoral species: *Carex pilosa*, *Aegopodium podagraria*, *Stellaria holostea*, *Pulmonaria* sp., etc.

An example of research on the status of the population of *E. helleborine* in constant sample plots in plantations of the Novhorod-Siverske Polissia is the study by Panchenko (2010). There are data about differently-oriented fluctuations in density of *E. helleborine* in conditionally primary light oak forest of *As. Mercurialo-Quercetum* (0.2 ind./10 m²) and derivative groups in pine forests with hazel, small-leaved and small-leaved-pine forests. Density of populations in light oak forests of associations of *Lathyro-Quercetum* ranges 6.1 ind./10 m² (Sytnovshchyna Tract of Kamianske Forestry) to 18.4 ind./10 m² in the territory of the Ichnia National Nature Park.

We saw that the level of development of generative specimens correlates with density of crowns of the tree stands, shrub stratum, structure of terrestrial cover, soil fertility, presence of leaf foliage, and young plants of *Acer platanoides* occurred in all the relevés. Satisfactory condition of studied populations in maple-linden spruce cenoses was observed. *E. helleborine* tolerates increased anthropogenic pressure in indigenous cenoses of broad-leaved forest ecosystems.

According to our data, the highest parameters of sizes of generative individuals were in population 2. Increase in density of generative individuals, high share of juvenile and generative plants indicates a “wave of restoration” (Rabotnov, 1950). In average-aged successive cenoses, population 1 is invasive, recovers, is currently having left-sided incomplete ontogenetic spectrum, where young pre-generative individuals (j, im, v) prevail. It is a young population, growing in the conditions of accumulation of leaf foliage that is able to hold moisture and increase soil fertility. The study determined that all examined populations in old indigenous cenoses (2, 3, 5) in the territory of the nature-reserve fund are normal (definitive), they may be considered relatively stable, ontogenetic spectra are incomplete, mostly with right-sided age spectrum, peaking at generative individuals of various stages. The large share of juvenile and generative individuals in populations 1–3 indicates their rejuvenation.

Left-sided incomplete ontogenetic spectra peaking at virgin individuals were described by Klimenko (2011) in the conditions of forest restoration successions (*As. Querceto-Pinetum coryloso (avellanae)-caricoso (ericetorum)*, *Betuleto-Pinetum coryloso (avellanae)-stellariosum (holostea)*). The author did not determine the overall number and density per

unit area. We determined that population 4 has lower number and incomplete spectra. The largest share of young generative and virgin individuals is now in the light oak forests.

Studies of influence of anthropogenic pressure indicated significant deviation from the basic spectrum and low density in population 6. There, *E. helleborine* experiences no heightened competition caused by other species of plants, and ecological-cenotic conditions did not reach the optimum level; we recorded an insignificant amount of foliage from broad-leaved species, since the accumulation of organics is the obligate limiting factor of recovery and spread of species, shading of trees (0.9) and shrub stratum (0.7) is sufficient. In the literature, there is an opinion (Panchenko, 2010) that decrease in light, increased share of broad-leaved species, crown density of the understory with *Corylus avellana* has directly caused the decrease in the number of *E. helleborine*. However, it is precisely forest ecosystems of broad-leaved forests with existing natural understory which are the primary natural biogeocoenoses of the studied species.

In the literature, there are data that intense impact of people (cutting, recreation, etc.) rapidly decreases numbers of plants. The first to disappear are juvenile and immature, and then adult plants, and in 4–5 years, a population can disappear completely. In particular, decrease in crown density to 0.6, caused by selective sanitary cutting of old *Quercus robur* trees in unprotected areas, is critical, having destructive effect on cenopopulations of forest orchids, leading to their complete disappearance from all the blocks (Yarova et al., 2020). Emergence of “windows” in crowns and rapid increase in light lead to decrease in moisture, deterioration of growing conditions and overgrowing by other species of plants. Therefore, we consider population 6 invasive-regressive – we recorded only virgin and generative individuals. We can state that populations exposed to anthropogenic impact are unstable, vulnerable.

Ontogenetic spectra of all the studied cenopopulations are incomplete – no seedlings spread by underground type of germination were found in the wild, while senile individuals were determined as those dying after the last blossoming, and therefore determining that individuals in this ontogenetic status needs more detailed studies. In particular, Smoliar & Smagliuk (2015) also notes a locality of *E. helleborine* with 5 individuals in the territory of the basin of the downstream Sula in a 70 year old broad-leaved oak-hornbeam forest of sprout origin with crown density equaling 0.9, understory accounting for 20%, herb stand of 75%, synusia of spring ephemerals: *Scilla bifolia*, *Corydalis solida*, *Ficaria verna*, *Anemone ranunculoides*, *Gagea lutea*, *G. minima*. Ontogenetic status of that population was not determined.

Right-sided, complete, two-peaked ontogenetic spectra of *E. helleborine* with dominance of young generative individuals were observed in the territory of nature-reserve fund with no recreation pressure (Russian Forest Reserve) (Vakhrameeva et al., 2014) in old oak-ash-hornbeam cenoses without expressed understory which are on grey forest soils. However, deterioration in the population and incompleteness of the spectra were observed in the territory of that reserve under anthropogenic impact. A number of studies provide data about recent dynamics of density of individuals of the species in cenoses under anthropogenic pressure of various extents. A number of studies (Solomakha, 2020; Tymochko & Solomakha, 2020; Solomakha et al., 2021) indicate data on dynamics of density of individuals in cenoses under various extents of anthropogenic pressure.

Conclusions

According to the results of monitoring studies of populations of *E. helleborine*, we observed disadvantages and perspectives of the study. To analyze generalized morphometric data, a several year long monitoring of populations is needed. Only long periods of study can reveal the dynamic of the range. Improved methods of selecting marker features of ontogenetic statuses would allow us to obtain data of dynamics of the status of populations in the conditions of Northeast Ukraine.

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