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

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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 bionindicators, according to Braun-Blanquet (1964), diagnostic species of the largest class of forest vegetation *Querceta (roboris) corylo-sa*, *Querceto-Pinetum corylo-sa*, *Aceroeto (platanoidis) – Tilio (cordatae) – Quercetum (roboris) agg. – Epipactis ge-nus – 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 morphologies of individuals taking into account morphometric data, ontogenetic and vital structures of populations, reproductive specifics of populations, 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 Palaeartic Eurasian nemoral species with broad ecological-ecotonic 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, understorey, 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 – Kremlia, Ivot, Svisa, Studenok), Svirzhka, Vita, Shloska (left tributary of the Ponarka), Osoa, Esmra (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% (Andreienko 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 (Prudyshchianske, Olynske, Dubovyske, Zemliankivskse, Slutske, 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 woodland, 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 & Shehylah-Sosonso, 2003) within Ukraine. According to physical-geographic zoning, it is a zone of mixed forests of Eastern-European physical-geographic province (Marnich 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 participation. 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 geophbic 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. Specifications of the biology were analyzed according to a number of studies (Varlygina & Vakhromeeva, 1998; Elifmov, 2004; Vakhromeeva et al., 2014). *Epipactis helleborine* is a herbaceous polycyclic plant with perennial sympodially overgrowing monochyclic vegetative-generative skeletal long-shoot axes. It is geophyte or axillary-rooted hemi-phyte of orchids before bud formation. The mycorrhizone is the initial shoot with scale-like leaf. We found no seedlings.

Juniwles (j) – plants starting from year 9, since appearance of first bell 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 1–2 rarely – 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: $H_{oa}$ – overall length (height) of vegetative shoot, (cm); $L_{oa}$ – general length (height) of generative shoot (cm); $N_{a}$ – number of developed shoot leaves (quantity); $L_{a}$ – leaf length (cm); $L_{a}$ – leaf width (cm); $n$ – number of veins, $L_{v}$ – length (height) of inflorescence (cm); $N_{f}$ – 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 |
|-------------------------------------------------------------|------------------------|----------------------------------------|------------------|
| Right bank of the Svyha River (Desna)                      | Svyhak vodyna           | 52.1892 33.3730                        | North of Hutko-Ozhynka village |
| Headwaters of the Svyha River (Desna)                      | Myhlav k vodyna         | 52.1883 33.7034                        | Northwest of Hutko-Ozhynka village |
| Headwaters of the Svyha River (Desna)                      | Yasina Halavunya        | 52.1894 33.7477                        | North of Kranychylka village |
| Right bank of the Svyha River (Desna)                      | Dubolitsia              | 52.2052 33.8084                        | Northwest of Lukashenkov village |
| Headwaters of the Ezma (Kleven)                            | Vedmetsza Ravine        | 51.7528 33.7864                        | South of Berenov village |
| Floodplain of the Ezma                                     | Plinicheva Ravine       | 51.6955 33.5444                        | Between Slout and Cherweno villages |
| Headwaters of the Ezma (Kleven)                            | Orliova                 | 51.7143 33.8636                        | Between Perovomosha, Pantolobor, Horile villages |
| Right bank of the Ezma River                               | Turovi Polynia glades  | 51.7551 33.7261                        | West of Slout village |
| Right bank of the Ezma River                               | Brod                    | 51.7438 33.7588                        | Southwest of Slout village |
| Headwaters of theMuraveina River                           | Shidhlyahutysya         | 51.7645 33.6047                        | North between Kudarnyvka and Hutka villages |
| Area between the Ezma and the Shostka rivers                | Borok                  | 51.7572 33.6369                        | Northeast of the Hutka khutir |
| Headwaters of theHlystanka (Ezma)                          | Pyshladino              | 51.6619 33.4338                        | Around Bilohryv village |
| Flood plain of the Ret River                               | Kravchenkova mountain   | 51.6328 33.5858                        | Northwest of Dobuvychylk village |
| Right bank of the Osoa River                               | Velykoe Bolot wetlands  | 51.7834 33.2522                        | Northwest of Klyshylk village |
| Right bank of the Ezma River                               | Kolodtsi               | 51.7361 33.5275                        | Between Pereomona and Kurlikino khutirs and Zernyan-ka village |
| Right bank of the Ezma River                               | Tytoviy gully          | 51.7253 33.6604                        | Northeast of Shevechenkov village |
| Flood plain of the Rekytsa (Ezma)                          | Nechaievsychna         | 51.6566 33.4580                        | West of Oholohy village |
| Right bank of the Ret River                                | Hruzky                 | 51.6027 33.4436                        | East of Hruzky village |
| Right bank of the Osoa River                               | Virovycha              | 51.7262 33.4105                        | Northwest of Voronizh |
| Right bank of the Osoa River                               | Voronizh               | 51.7511 33.4017                        | South of Masykov village, west of Voronizh |
| Floodplain of the Ivotka River                             | Lomlenka               | 51.9998 34.1210                        | North of Lomlenka village |
| Left bank of the Ivotka River                              | Velykoe Voloka         | 51.9052 33.5619                        | North of Myronivka village |
| Headwaters of the Shemenka (Ivotka) River                  | Nepliusevychyna        | 51.9665 34.0406                        | West of Munchyhyno Buda village |
| Area between the Ivotka and the Svesa rivers               | Kryvi Kishi            | 51.9442 33.9335                        | North of Svesen town |
| Left bank of the Kremlia River (Ivotka)                    | Radya                  | 51.9804 33.8500                        | Outskirts of Yampyl, near Nepiauevke village |
| Right bank of the Ivotka River, between the Kremlia and the Ivotka rivers | Kremlia vodnya          | 51.9766 33.8480                        | Around Chryzyhyvuku khutir and Nepliauevke village, north of Yampyl |
| Left bank of the Svesa River                               | Pustba                 | 51.9477 33.7866                        | West of Ohl}], east of Yampyl |
| Left bank of the Shehinka River (Ivotka)                   | Demianivske            | 51.9566 34.1316                        | East of Demianivske khutir |
| Headwaters of the Svesa River                              | Krivychyk               | 51.9041 33.7766                        | Southwest of Ishana village |
| Right bank of the Ivotka River                             | Novopokrovskoe         | 52.0080 33.7580                        | North of Belovsky and Derazhnya villages |
| Right bank of the Ivotka River                             | Hresty                 | 52.0421 34.0297                        | East of Chukivka village |
| Headwaters of the Usok rivers                              | Dovha Loza             | 51.9840 33.6073                        | Outskirts of Usok village |
| Right bank of the Ivotka River                             | Khutorysshe            | 51.9829 33.5460                        | North of Antonivka and Ivot villages |
| Right bank of the Ivotka River                             | Radlob Bir cernyi forest | 51.9592 33.4449                       | Between Pohreboky and Ivot villages |
| Headwaters of the Laniaonivka River                        | Syntykiv Klyn          | 52.0241 33.6819                        | Between Shatyshchylk and Antonivka villages |
| Headwaters of the Laniaonivka River, right bank of the Ivotka River | Dibrhove               | 52.0036 33.5869                        | North and northwest of Antonivka village |
| Right bank of the Ivotka River                             | Khutorysshe            | 51.9921 33.5460                        | Between Antonivka and Ivot villages |
| Right bank of the Usok River, between the Usok and the Ivotka rivers | Puryviv Zrub           | 51.9305 33.6696                        | North of Paielvka, Usok, Oliyno villages |
| Between Ivotka and the Shoshka rivers                      | Kirovka Dacha          | 51.9071 33.4125                        | Between Obrazhievska and Myronivka villages |
| Floodplain of the Svyha River (Budyhyn)                    | Dubova Korna           | 52.1272 33.9008                        | Between Kamianinka, Shulyakynya and Snyte villages |
| Floodplain of the Shoshka River (Poninka, Litra)           | Shatryshchyna          | 51.8111 33.8730                        | North betweenHora and Shatryshchyna khutirs |
| Headwaters of the Ezma (Kleven)                            | Kryvenkove             | 51.8038 33.8424                        | Between Kryvenkove village north of Ivaschhenkove village |
| Right bank of the Shoshka River                            | Bukatovskychyna        | 51.8340 33.6245                        | Between Makove and Taranivka villages |
| Right bank of the Poninka River                            | Turovychyk             | 51.8297 33.7891                        | North of Dolyavka village |
| Right bank of the Shoshka River                            | Kryvytschyzhko        | 51.8427 33.7733                        | North of Taranivka village |
| Right bank of the Shosha River                             | Miliuty Forest          | 51.8867 33.3759                        | Between Lazaryvka, Obrazhievska, Bohdna village |
| Left bank of the Shosha River                              | Ulytsnye               | 51.8622 33.3643                        | South of Bohdana village |
| Right bank of the Shosha River                             | Myhalivska Dacha       | 51.1122 33.3722                        | North of Makove and Hanalivka villages |
| Headwaters of the Usok River, area between the Shoshka and the Ivotka rivers | Dovha Loza             | 51.9154 33.6422                        | South of Paielvka and Usok villages |
| Left bank of the Desna (Dnipro) river, area between the Shostka and the Osoa rivers | Hlyboly Kolodiac       | 51.8086 33.1327                        | Between Tymanivka and Sobych villages |
| Left bank of the Desna (Dnipro) river, area between the Shostka and the Osoa rivers | Velyky Bir cernyi forest | 51.8095 33.1759                        | Between Tymanivka and Sobych villages |
| Left bank of the Desna (Dnipro) river                      | Kryowska Dacha         | 51.9052 33.5619                        | West of Myronivka village |

Categories of the populations were determined according to the generally adopted methods (Uranov, 1975, 1977; Smirnova 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-genetic peculiarities of forest ecosystems. Geobotanical descripi
tions were analyzed, syntaxa were distinguished and identified according to "Prodromus of vegetation in Ukraine" (Dubynà et al., 2019) and “Green Book of Ukraine” (Sheylych-Sosonko & Andrienko, 1987; Sheylych-Sosonko et al., 2002; Diduluk, 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 elder buckthorn-grass (light oak forests) and disturbed forests (birch-pine hazel forests).

Table 2

| Administrative location, protection category | Group according to dominant floristic classification | Age of tree stand, years | Density of tree crowns | Density of under tree crowns | Projective cover of grass stand, % | Density, ind/10m² |
|---------------------------------------------|---------------------------------------------------|-------------------------|-----------------------|-----------------------------|----------------------------------|------------------|
| Verhnievomskansky Reserve, Slucke Forestry, Tourov Polissia, block 77 | Querco-Quercetum coryllosa/Corylo avellanae-Pinetum | 60–70 | 0.8 | 0.7 | 40 | 3.3 |
| Verhnievomskansky Reserve, Zemelianivske Forest, Hutianske (Kökoliths) Tract, block 22, compartment 14.1 | Betulo-Quercetum coryllosa/Carici pilosae-Quercetum roburis | 90–110 | 0.7 | 0.8 | 40 | 10.0 |
| Dubovskoye Forest, block 65 | Querco (roboris) coryllosa/Carici pilosae Quercetum | 100–120 | 0.8 | 0.7 | 25–30 | 6.5 |
| Protected Tract Pidvidotskovo-Chuikivska Dacha. Chuikivske Forest, block 32, compartment 18 | Querco-Quercetum coryllosa/Pinetum | 90–100 | 0.8 | 0.6 | 50–60 | 1.4 |
| Reserve Usynskiy, Shnotkynske Forest, block 33, compartment 6 | Querco-Quercetum coryllosa/Corylo avellanae-Pinetum | 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 | Type I | Leaves of the middle formation | Type II | Type III |
|-----------------------|--------|-------------------------------|---------|---------|
|                       | Ns, quantity | L, cm | L, cm | Ns, quantity | L, cm | L, cm | Ns, quantity | L, cm | L, cm |
| j                     | 0       | 0.0 | 0.0 | 1–2 | 3.5 | 1.2 | 0 | 0 | 0 |
| im                   | 1       | 1.6 | 0.7 | 3–7 | 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 | 1.0 | 4–5 | 9.0 | 3.0 | 1–4 | 1.2 | 0.2 |
| g                   | 1       | 3.5 | 1.0 | 4–5 | 10.0 | 3.0 | 1 | 2.2 | 0.5 |
| g                  | 1       | 6.8 | 0.7 | 6–7 | 10.6 | 6.0 | 1–2 | 2.2 | 0.9 |
| g                 | 1       | 3.8 | 0.6 | 5–7 | 12.5 | 6.5 | 1 | 2.2 | 0.9 |
| s                      | 0       | 0.0 | 0.0 | 0–6 | 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 | Hsup, cm | Formation of leaves apex (involute) | Internodes | Vegetative shoot | false whorl | Inflorescence |
|-----------------------|----------|------------------------------------|-------------|------------------|------------|--------------|
|                       | Ns, quantity | L, cm | L, cm | elongated | present | absent | short | elongated |
| j                     | 8.0      | –     | –     | –     | –     | –     | –     | –     |
| im                   | 14.0      | –     | –     | –     | –     | –     | –     | –     |
| v                    | 17.0      | –     | –     | –     | –     | –     | –     | –     |
| vv                   | 30.5      | 2.4   | 2.5   | 0.5   | –     | –     | –     | –     |
| g                   | 25.5      | 13    | 2.3   | 1.2   | –     | –     | –     | –     |
| g                 | 55.0      | 33    | 2.2   | 0.5   | –     | –     | –     | –     |
| g                 | 32.5      | 6     | 2.4   | 0.9   | –     | –     | –     | –     |

Note: “–” absence of the indicated morphological features in leaves of apex formation (involute) 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 m² | Proportion of age groups, % |
|------------|---------------------------------|-----------------------------|
|            | j | im | v | g | g | g | 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 Querco-Quercetum 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 plants of Q. robur, Betula pendula, Acer platanoides, Tilia cordata, Ulmus minor, 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. nessensis, Padus avium, Acer negundo, Amorpha fruticosa occur. The floristic “kernel” of the herbaceous-shrub layer is mainly plants of Q. robur, Betula pendula, Acer platanoides, Tilia cordata, Ulmus minor, 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. nessensis, 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 Sorbus holostea (20–30%), subdomi-
nants were Carex pilosa, Pulmonaria obscura, Glechoma hirsuta, Lathyrus vernus, Trientalis europaea. This censuses 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 Quercetum-Pinetæ corylosa is a typical old indigenous forests of the Polisia, where E. helbovirine, Neottia nidus-avis, Primula veris, Lilium martagon grow in floristically-rich sites.

In the studied region, rare censuses of such type have been described and are protected in Bohdanivsky and Voronizky Reserves (Ass. Querco-Pinetæ Cl. Querco-Fageteæ). Total number of this population is almost impossible to determine, because it potentially may be over 1,000 speci-
mens per general area of compartment or block. Therefore, we should consider the average density. At the distance of 10 m from the node, ave-
dage 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. helbovirine. The popula-
tion was young. Age spectrum was normal, incomplete, left-sided mono-
modal 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 censuses are presented in Table 6.

Cenopopulation 2 of E. helbovirine. Late-successional forest. It is an area of birch-pine forest with hazel Betuleto-Pinetæ corylosa (Carici pilosae – Quercetum robur) (Mercurialio-Quercetum, Aceri campestris – Tilietum cordatae) aged 90–110 years, which comprises Pinus sylvestris, where leaved species are undergoing recovery. Tree stand 55D, 82D: Pinus sylvestris of 30–32 m height, with 38–42 cm diameter. Betula pendu-
dula was 24–26 m high, 22 cm in diameter, and crown density equaled
0.7–0.8. The understory (0.6–0.8) was composed of Corylus avellana.
The floristic “kernel” of herbaceous-shrub stratum was represented by
Aegopodium podagraria. This censuses 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-Pinetæ corylo-
sa – typical old indigenous forests in Polisia. In the region, censuses are protected in the territory of Dibrova and Kniazhjetsky Landscape Reserves of local significance and Pidvostok-Chuhtivska Dacha and Dilahtanka 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. Incom-
plete (no seedlings and sentile 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. helbovirine. Conditionally ancient forest, typi-
cal 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–3+D, crown densi-
ity 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
sizes, namely Acer platanoides, Tilia cordata. The understory’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, Epimedium acuminata, Sorbus aucuparia, Rubus idaeus, Frangula alnus, Populeto-Querceto-Pineta franguloso graminosum. 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 indi-
viduals (50%). It is a mature population, transitional to ageing.

Cenopopulation 4 of E. helbovirine. Conditionally ancient forest, area of
sun-fit floristically rich group of associations Quercetum corvallari-
osome, Q. petriodisum, Populeto-Quercetum frangulosu graniniosum. 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 understory 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, Epipsachis helbovirine, Platanthera bifolia, Pers-
cedanum cernuum, Campanula cernueta, Asterol amelli, Digitalis grand-
diflora, Iris hungarica, Laserpitium pratense, Genista germanica, Serratula tinctoria, Thalictrum aquilegifolium, Primula veris, Dianthus stenocolx. According to modern schemes of ecological-floristic classifi-
cation, the groups belongs to Ass Lathyro nigri-Quercetum roburis Bau-
lodikol et Solomoshch 2003 Cl Quercetcea subpentae-petraeae Jakus
(1960) 1961 and are close to the Central-European association of Potentil-
ae albae-Quercetum petraeae Libb. 1933 group of Quercion petraeae, in the
herbaceous stratum of which, meadow-steppe and grass species domi-
nate Cl. Querco-Fageteæ Br.-Bl. et Vlieger 1937, described from
southern parts of Polisia of Poland and Ukraine. In the studied region, it
is protected in the Prudyshchansky (block 53) and Kremliansky (block 58) forstries of Yampl district, Verhnioesmansky 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. helbovirine. 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) – Tilio (cordatae) – Querceto (roboris)
aggepodiosum. Acereto-Tilio-Quercetum caricion (pilosæ). In the
Eurasian system: W1.22 East-European mesophyllous eutrophic forests
of common oak and small-leaved lime of the forest zone. Syntaxonomic
composition: Acereto (platanoidis) – Tilio (cordatae) – Querceto (robo-
ris) aggepodiosum, Acereto (platanoidis) – Tilio (cordatae) – Quercet-
com (roboris) xerocaricion (pilosæ), Mixeto-Quercetum xerocaricion (ursini), Cl. Querco-Fageteæ. This population includes Populetæ tremulae, represented by associations of Populetæ (tremulae) – coryloso (avellani) xerocaricion (pilosæ). 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 understory is 0.4–5–6 m high, formed by Corylus avellana (0.4), singularly – Euonymus verrucosa, and young plants of Tilia corda-
ta. Herbaceous cover is 60%, with dominant Carex pilosa accounting for
30%. In the region, it is also protected in the Bohdanivsky Reserve, Tu-
rovshchyna and Krynynchych forest tracts. In the area of 200 x 6 m, we
observed over 45 specimens. Normal (definite) 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. helbovirine. 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-Pinetæ corylosa/Carici pilosæ-Quercetum) with scattered Populus tremula, Betula pendula, Picea abies. The understory is composed of Coryle
avellana, with 0.6 density. Terrestrial cover is almost without mosses, the
structure of the censuses has been disturbed by presence of synanthropic
species. Young plants are Acer platanoides, Tilia cordata. Among natural
nemoral species, there are Aegopodium podagraria, Stellaria holostae, Asarum europaeum. This population is the smallest by spread area
(400 m²), number (17 individuals) and density (0.1 ind/10 m²). The on-
ogenetic 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 com-
position and structure of typical primary censuses that have become rare.
At the same time, cenicotic vulnerability is related to floristic. Many species
of forest orchids are rare not only in Ukraine (Timchenko, 1996; Efimov,
2004; Pros, 2010; Lukba, 2018; Fatyrya, 2018a; Calceo & Bazzicacu-
po, 2020; Efimov, 2020; Khapagan, 2020; Popovich et al., 2020; Kirillova &
Kirillov, 2021). Species of Epipactis genus are characterized by vulnerability in Central Europe (Melnik, 1996; Molnár & Szabók, 2012; Djerdević, 2016), Caucasus (Perebora, 2011; Fateryga et al., 2018b), Russia (Efimov, 2004; Vakhromeeva 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 hypogeous survival of orchids (Light & MacConnell, 2006). This reflects significance of indigenous forests. Our data about floristic discoveries of E. helboerine in the territory of Shostka geobotanical district (Chomous & Andriyenko, 2004; Chomous, 2005, 2006) are specifically related to old censuses. 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 forests areas of the region were broad-leaved associations of As. Mercurialo perrenis-Quercetum roboros Bulokhov & Solomeshch 2003 group Querco roboros-Tilion ellipsoides Solomakha et et al. 1993 ex. Bulokhov et Solomeshch 2003; with light oak forests of As. Lathyro-Quercetum of class Querceta pseudoet phyllistis Jakacs (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, Vrhnishemansky, Velky Bir, Dibrova Reserves, etc.) at the locations of primary censuses, which at the age of 60, at the stage of restorative successions, have formed As. Corylo avellaneae-Pinetum sylvestris Bulokhov & Solomeshch 2003 (group Querco-Tilion) and As. Querco-Ficevetum (W. Matuszkiewicz 1952) W. Matuszkiewicz et Polak 1955 (group Melico natisico-Piceion abietis (Killand-Lund 1981) Onyshchenko 2005 prov.). At such plots, the dominant species in the tree stand is Pinus sylvestris, and ctenotopic 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 podagrae, Stellaria holostea, Pulmonaria sp., etc.

An example of research on the status of the population of E. helboerine in constant sample plots in plantations of the Novhorod-Siverskoe Polissia is the study by Panchenko (2010). There are data about differentially-oriented fluctuations in density of E. helboerine 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 (Sytvosvychyva 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 censuses was observed. E. helboerine tolerates increased anthropogenic pressure in indigenous censuses 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 censuses, 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 censuses (2, 3, 5) in the territory of the nature-reserve fund are normal ontogenetic successions (As. Querco-Pinetum coryloso (avellanae)-caricosum (ericetorum), Betuleto-Pinetum coryloso (avellanae)-stellariosum (holostei)). 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. helboerine experiences no heightened competition caused by other species of plants, and ecological-ontogenetic 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. helboerine. However, it is precisely forest ecosystems of broad-leaved forests with existing natural understory which are the primary natural biocoenoses 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, Smolar & Smaglik (2015) also notes a locality of E. helboerine 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%, suanua of spring ephemeroptera: Scilla bifolia, Corydalis solida, Ficaria verna, Andromone ranunculoides, Gagea letea, Gi minima. Ontogenetic status of that population was not determined.

Right-sided, complete, two-peaked ontogenetic spectra of E. helboerine with dominance of young generative individuals were observed in the territory of nature-reserve fund with no recreation pressure (Russian Forest Reserve) (Vakhromeeva et al., 2014) in old oak-asl-hornbeam censuses 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 censuses under anthropogenic pressure of various extents. A number of studies (Solomakh, 2020; Tymochko & Solomakh, 2020; Solomakh et al., 2021) indicate data on dynamics of density of individuals in censuses under various extents of anthropogenic pressure.

Conclusions

According to the results of monitoring studies of populations of E. helboerine, 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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