Features of Spatial and Temporal Dynamics of Tuberous Orchid Populations

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Abstract—Features of the long-term fluctuation dynamics of populations of tuberous orchids (*Neottianthe cucullata* and *Dactylorhiza incarnata*) growing under various phytocenotic and climatic conditions are shown as a result of the functioning of a mechanism providing population stability in a heterogeneous habitat. The capability of the population to occupy microsits with favorable conditions determined by the dynamics of climatic factors, the abiotic environment, and interspecific relations has been shown. The irreversible dynamics of tuberous orchid populations determined by demutative and digressive successions in plant communities and influenced by abiotic, biotic, and anthroogenic impacts results not only in the reduction of population magnitude and density, but also in violations in the spatial and ontogenetic structure of the population. A correlation between the population magnitude and climatic factors has been evaluated using a correlation coefficient, the value of which was high for generative plants of forest species (*N. cucullata*) and for juvenile plants of meadow species (*D. incarnata*).

INTRODUCTION

In the ecological context, vegetation, like the landscape as a whole, is a complex mosaic of various elements and reflects the mosaic of habitats, populations, and communities, each corresponding to its own picture (Allen and Hoekstra, 1990). The borders of individual elements are rather continual, which determines the objective troubles of separating them; according to Rozenberg et al. (2007), "...it is also important that both temporal and spatial scales are specific and differing for different elements of the ecological system." In connection with this, an ecological and landscape analysis of the spatial and temporal dynamics of populations and its results depend on the dimensional scale of the corresponding object of study.

Population dynamics is determined by the direction, duration, intensity, scale, and reasons for temporal changes. The occurring processes may represent *irreversible* (succession) and *reversible* (fluctuations) population changes (Diggle, 1985). A character of the responses of populations to external impacts allows us to talk about the manifestation of two mechanisms of their stability: stability as an ability to keep a relatively constant state under the influence of "nonfatal" factors and resistance as an ability to maintain equilibrium via deviations and returns to the initial state (Begon, 1986; Zaugol'nova, 1994). In this case, a population has some conservative features intended to maintain the constancy of the system (for example, reproductive organs of plants, their quantitative and qualitative characteristics, life-form structure and related dominating reproduction types, ontogenesis type, and ontogenetic and spatial–ontogenetic structure) and having a small amplitude of changes. Dynamics, or "compensatory" features providing the responses to environmental changes, include the magnitude, density, and vitality of a population, as well as the projective cover and the corresponding spatial contour, i.e., the space occupied by the population. Usually, a joint change of some population characteristics caused by endogenous and exogenous factors is observed.

Long-term observations of tuberous orchid populations showed a high-level dynamics of their magnitudes, as well as age and vitality structures (Vinogradova, 2000; Batalov, 2007; Suyundukov et al., 2008; Blinova, 2009, 2016; Kazazaeva, 2009; Marakanova, 2011; etc.). Blinova (2016) described the shortening of the ontogenesis of tuberous orchids as an evolutionary process caused by the *r* strategy; this feature is especially noticeable at the habitat border and facilitates a rapid development and frequent dislocations of populations to areas with more favorable conditions. After the analysis of a 25-year dynamics of the magnitude and age structure of *D. fuchsii* populations and the

impact of various factors on these populations, Vakhrameeva (2006) supposed that these populations are influenced mainly by weather conditions, as well as zoogenic, phytogenic, and anthropogenic factors. Many authors emphasized the lability of orchids, as well as their ability to grow in a wide range of abiotic factors and to turn to the nonflowering or secondary dormancy state underground to survive over an unfavorable period (Light and McConaill, 2006; Vakhrameeva et al., 2008). Nevertheless, irrespective of their lifeforms, orchids are still the rarest plants of the moderate zone despite the wide occurrence of mycorrhyzal fungi, which are their consorts. This fact determines the relevance of long-term complex studies to determine a potential space of orchid populations including not only the seed bank, but also protocorms and secondary dormant plants.

Fluctuation dynamics is well described in the model of a "buffer" population localized along the gradient of any factor; the model was proposed by Whitteker (1977). Studying a spatial mosaic of orchids, Law et al. (2009) concluded that the data on the current spatial arrangement of plants can not provide information about the occurring ecological processes ("these are illusions only"). The authors consider the necessary condition for a complete analysis is the study of dynamics of temporal changes of the spatial structure. Dodd (2011), who studied the spatial structure of *Anacamptis morio* populations for 10 years, described aggregations of plants located at a distance of 40 cm from each other. These aggregations were observed during the entire period under study, though they varied in size. According to the author's opinion, the formation of these plant aggregations is determined by the features of their reproduction. Jacquemyn and Vandepitte (2009), who studied the variability of the spatial and age dynamics of *Orchis mascula* populations, reported a weak, but strongly confident, regularity of their spatial structure, which represented the ability to form aggregations of either juvenile or generative plants. The authors also mentioned that the expansion of seeds of terrestrial orchids is limited by several meters around the maternal plant, which probably is the reason for aggregation formation. A similar tendency to aggregation formation was described for *Cymbidium goeringii* populations in the absence of anthropogenic impact (Chung and Nason, 2007). The authors of this study proposed using spatial distribution metrics as an indicator of anthropogenic changes.

The main purpose of our study was to elucidate the reasons and features of spatial and temporal dynamics of tuberous orchid populations. To do this, the following tasks were stated: to analyze the data of a long-term monitoring of the spatial and ontogenetic population structures, reveal the features of the fluctuation and irreversible dynamics, and determine the mechanisms of population stability of rare orchid species under various conditions.

We consider the dynamics of a *spatial and temporal* structure of populations as a continuous series of changes in the spatial and ontogenetic structure of microloci in a certain scale of the space-time continuum occurring within a certain time interval (5—10—15 years) in the same phytocoenosis.

According to the behavioral strategy in phytocoenoses, orchid plants are patients requiring specific ecocoenotic conditions. However, in the case of weak competition or stress situations, tuberous orchids sometimes show themselves as "false" or "phytocoenotic" explerents (due to high seed productivity) or as ecotopic patients (under conditions of depleted calcareous, sabulois, or alkaline soils). It is supposed that the strategy and the lifeform predetermine population structure features. *R* strategists, to which tuberous orchids belong (Fardeeva, 1997; Willems et al., 2003; Ishbirdin et al., 2005; Blinova, 2009), are characterized by active dynamics of the population magnitude and density with often the prevalence of juvenile groups and, apparently, by rather dynamic spatial contour of a population determining the potential space occupied by the species and reflecting the stability of the population under changing environmental conditions.

In this study we analyzed the spatial and temporal dynamics of coenopopulations of *Neottianthe cucullata* (L.) Schlechter growing under conditions of a protected area with minimized anthropogenic impact and *Dactylorhiza incarnata* (L.) Soy growing under city park conditions.

MATERIALS AND METHODS

This study is an analysis of the spatial and temporal dynamics of four coenopopulations (CPs) in 2005—2016 (Table 1).

Their long-term monitoring was based on the multiple mapping of plant locations with the indication of their ontogenetic stage.

The spatial and ontogenetic structure was visualized by the mapping of local population densities using a radial basis function (Diggle, 1985; Baddeley et al., 2015). The whole mapped area is covered with a regular grid and, for each cell, the density of a species is determined as the function of a number of specimens located in the neighborhood of the cell. From the point of view of population analysis, it is very important that such density visualization makes it possible to reveal the magnitude, continuity, or fragmentariness of the population field (a term proposed by E.L. Lyubarskii (1976)), to determine the space occupied by the population and to formulate hypotheses about the observed processes.

The scale of a spatial heterogeneity was evaluated using Ripley's $K(r)$ function (Ripley, 1977) and pair correlation function (Stoyan, D. and Stoyan, H., 1994; Illian et al., 2008; Wiegand et al., 2013).

Table 1. Characteristics of the studied populations

Specues	CP No.	Coordinates	Habitat
N. cucullata	1	N 55.95 E 48.83	VKNR, spruce forest edge
N. cucullata	2	N 55.52 E 48.45	VKNR, burchwood on the road bank
N. cucullata	3	N 55.53 E 48.43	VKNR, pine forest edge
D. incarnata	4	N 55.81 E 49.10	Sedge—grass meadow in the floodplain of the Kazanka River

(CP) coenopopulation; (VKNR) Volga-Kama Natural Reserve.

All calculations were performed using spatstat software (Baddeley et al., 2005) and the R statistical package (R Development Core Team, 2006).

RESULTS AND DISCUSSION

During long-term studies of the population dynamics of tuberous orchids, we often revealed their fluctuational changes caused by climatic factors, especially variations in the temperature and total precipitations during a vegetation period; these factors also indirectly influenced the abiotic constituents of the ecotope. Along with frequent fluctuations in the population magnitude and density under different ecological conditions, we also observed processes of spatial contour changes occurring in the form of translocation or changes in the spatial pattern of coenopopulation loci with the corresponding dynamics of their number and density. Paraphrasing the term proposed by Reymers (1990) for migrations of animals, we determine "micromigrations" in the space of tuberous orchids as a periodical or nonperiodical horizontal translocation of population members occurring within a long period towards favorable habitats associated with different parts of the meso- and microrelief or plant synusia; this translocation occurs due to diaspores, which form a bank of seeds and protocorms around the existing microloci and the appearance of secondary dormancy in vegetating members of the population or the dormancy release.

To illustrate this type of dynamics, we consider results of a study of *N. cucullata* populations located on the territory of the Volga-Kama Natural Reserve at the edge of a pine—spruce green moss forest (CP1, Table 1, Fig. 1). Illumination of the population was heterogenous; there were both shaded and open microsites located under the forest canopy and at the forest edge, respectively. To evaluate the growing conditions at different microsites, some abiotic characteristics were measured in the period from July 15 to 17, 2016, at 2:00 p.m. In the case of a shaded microsite, the average illumination, temperature, and air humidity were 3120 Lx, +22.2°C, and 69.2%, respectively. For open microsites, these values were 15766 Lx; +22.9°C, and 68.9%, respectively.

During the period of study, the number and density of plants reduced from 205 (2005) to 67 (2016); such a decrease was caused mainly by a drought that occurred in 2009−2011. This climatic anomaly resulted in a CP migration to the more shaded and wetter part of the cowberry—billberry—green moss synusia. The largest part of the population was initially concentrated on the illuminated area (Fig. 2a), where highly competitive *Vaccinium myrtillus* and *V. vitis-idaea* were almost absent. The droughty period stimulated a CP division into several microloci. In 2009, the largest part of vegetating plants concentrated in a shaded area (Fig. 2b), characterized by a high projective cover of mosses and higher air and soil humidity. The population field of *N. cucullata* on the illuminated site became fragmented due to the decreased number and density of plants. By 2012, which was characterized by increased precipitations and air humidity, the population field started to return to the initial pattern, and the maximum *N. cucullata* density was observed on the illuminated site (Fig. 2c). Nevertheless, consequences of the droughty period still gradually affected the population: by the beginning of 2012, almost all undergrowth of *Picea fennica* growing on the forest edge withered (Fig. 2d), the number and projective cover of *V. myrtillus* and mosses decreased, *Convallaria majalis* started to actively grow, and the clear border between the forest and the forest edge was partially leveled. In the CP dynamics we observed a drop in average density from 8.4 (2005) to 1.88 (2016), while fluctuations in the CP magnitude in different microsites occurred synchronously with the changes of climatic factors (Fig. 1).

During 11 years of observations, the type of spatial and ontogenetic structure of *N. cucullata* CP1 did not significantly change; it still remained discrete-continual with low- and high-density aggregations, the size of which varied within 0.3−0.4 m (Figs. 2c, 2d), and its ontogenetic structure, which included all age groups, remained unchanged within the area of the elementary demographic unit (~3 m²).

In general, such a dependence on climatic factors is typical for forest orchids: there is a significant positive correlation between the number of generative plants and the amount of precipitations and air humidity, while a negative correlation of this parameter was observed with high temperatures and number of days without precipitations. Due to the small size of juvenile plants, they are often partially buried in the mossy tussock or covered by leaves of generative plants; this effect is enhanced by the "group effect," the i.e., for-
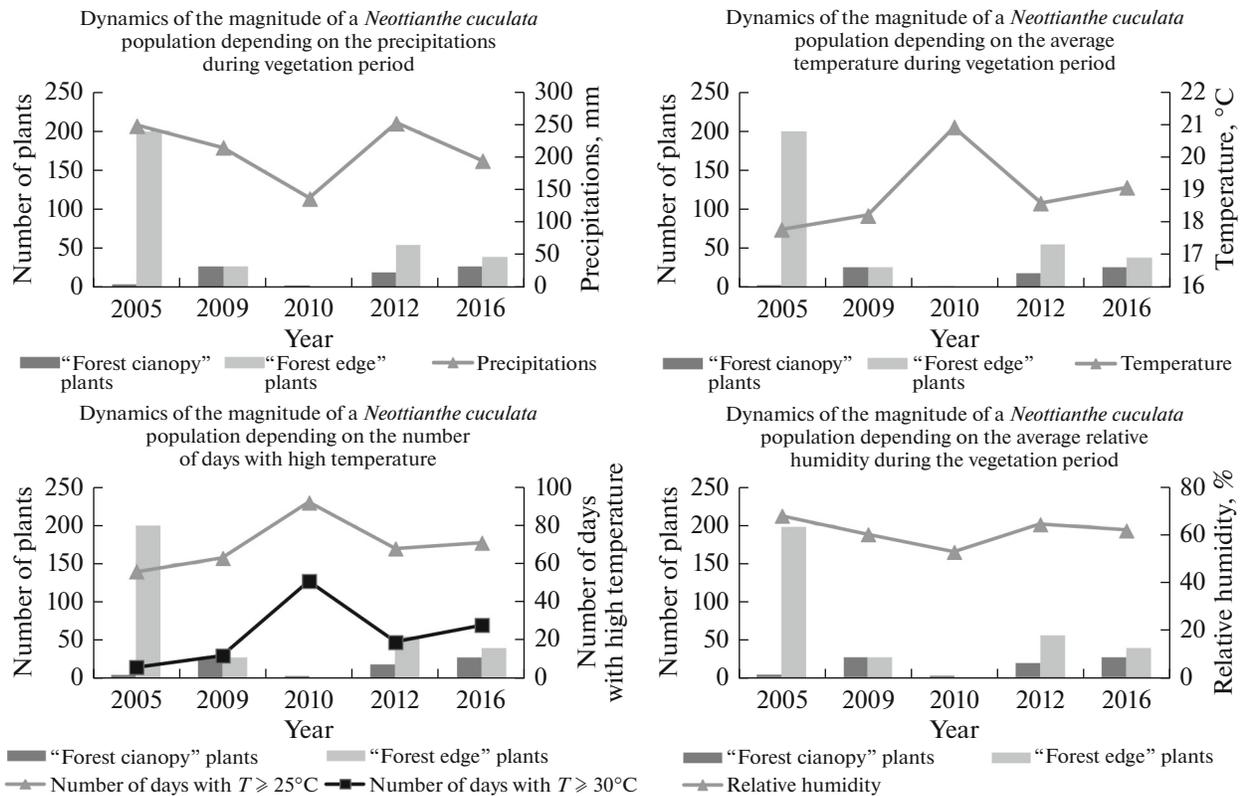
Fig. 1. Climate-dependent dynamics of the *N. cucullata* magnitude in different microsites (forest canopy/forest edge) during the vegetation period (May−September).

mation of large aggregations. Due to these features, juvenile plants are less dependent on climatic factors.

Changes in the magnitude and spatial structure of populations are determined by a complex of different factors, often including digression and demutation processes occurring in phytocoenoses. The rate of these processes may be determined by both anthropogenic and climatic impacts. Let us consider two CPs of *N. cucullata* (CP2 and CP3) as an example of the population dynamics determined by a complex impact of climatic, anthropogenic, and phytocoenotic factors, which caused differences in the development of two coenopopulation loci (Table 1).

In 1990s, both these CPs formed one population associated with a bumpy area of a cowberry−mossy pine forest located along the road crossing the territory of the nature reserve. In 1990s, because of road repair and enlargement, this population was divided into two coenopopulation loci (CLs) located on a road bank (CP2, Fig. 3) and on a hillock (CP3, Fig. 4) located at a distance of 7−10 m from the road. In the beginning, the age and spatial structures and the magnitude of both CLs were similar.

Within 10 years, a young grassy birchwood with linden undergrowth and small mossy curtains was gradually formed on the road bank (CP2). Along with the forest and meadow grasses, the herbage also included

forest plant species, such as *Convallaria majalis*, *Carex rhizina*, *Luzula pilosa*, *Viola rupestris*, and *N. cucullata*. In 2005 we observed an outbreak of *N. cucullata* in the CL located on the road bank (CP2): the number of plants reached 366 with an average density equal to 12.2 (Fig. 3a). Apparently, there was a process of species invasion into a rather unoccupied territory; juvenile plants made up 80% of the total number of plants. However, permanent drifts of sand, macadam, and garbage from the road destroyed the mossy carpet; during droughty periods (2009−2011), the habitat of the lower part of the bank was destroyed, which significantly disturbed the state of the CL. The number of plants reduced to 24 in 2012, their density was 0.8 plant/m², and the continual pattern of the population field became fragmentary (Fig. 3c). The spatial and age structure also changed, and the mutual arrangement of generative and other plants became casual (Fig. 3c). The presence of all ages in the ontogenetic CP structure was disturbed. Under such conditions, it was impossible to determine the area of the elementary demographic unit.

At the same time, the minimization of anthropogenic impact within the natural reserve (first and foremost, the absence of the trampling and recreational activity) provide a normal reforestation process on the disturbed areas. The disastrous drought resulted in an
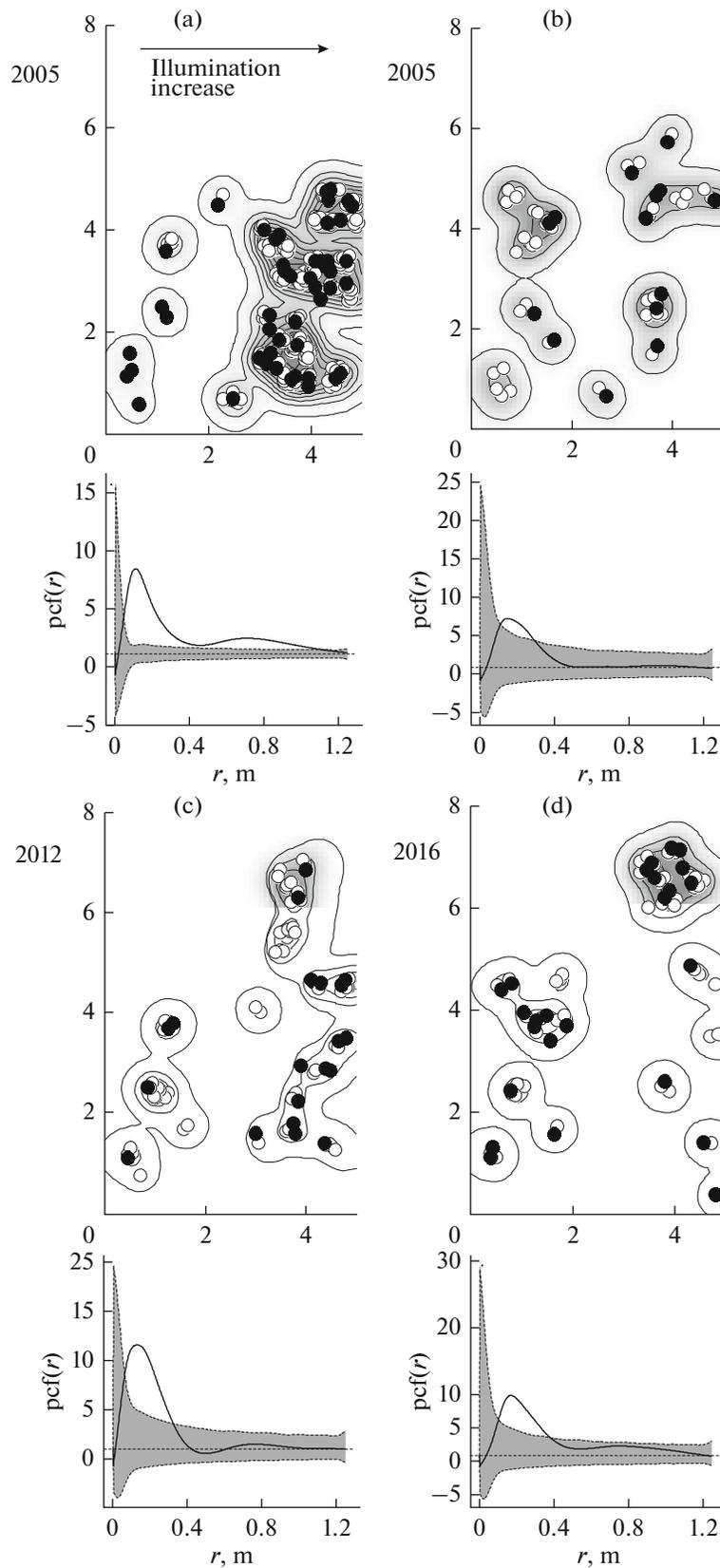
Fig. 2. Dynamics of the spatial structure of *N. cucullata* CP1: maps and pair correlation function. (a) 2005; (b) 2009; (c) 2012; and (d) 2016. Generative and juvenile plants are indicated by black and white dots, respectively. The first contour corresponds to the density of 1 plant/m^2; further steps are equal to 5 units. Diagrams show the pair correlation function for arrangement of all plants of the population. The area of the null hypothesis (random spatial arrangement of plants), or randomization "envelope," is shown in gray.
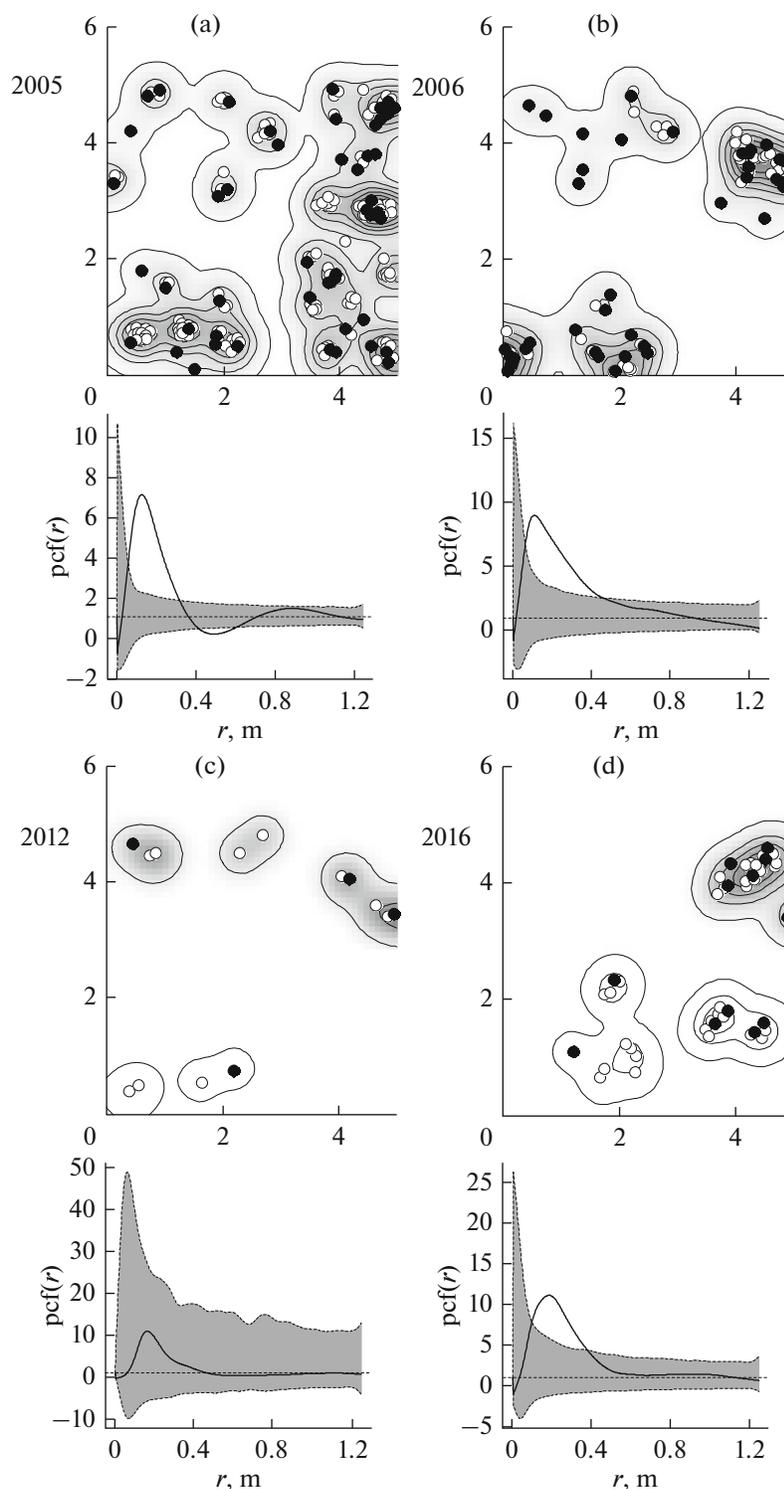
Fig. 3. Dynamics of the spatial structure of *N. cucullata* CP2: maps and pair correlation function. (a) 2005; (b) 2009; (c) 2012; and (d) 2016. Other indications correspond to those in Fig. 1.

increased succession rate: young birchwood quickly dried out and was replaced by forest grasses (*Convallaria majalis* and *Pteridium aquilinum*) and the linden and pine undergrowth, which formed a primary canopy. By 2016, the CP2 of *N. cucullata* was recovered; its magnitude increased to 44 and most plants were concentrated in microloci, which were the farthest from the road. The discrete-continual type of the spatial structure of generative groups and all plants was recovered (Fig. 3d) (Fardeeva, 2016).
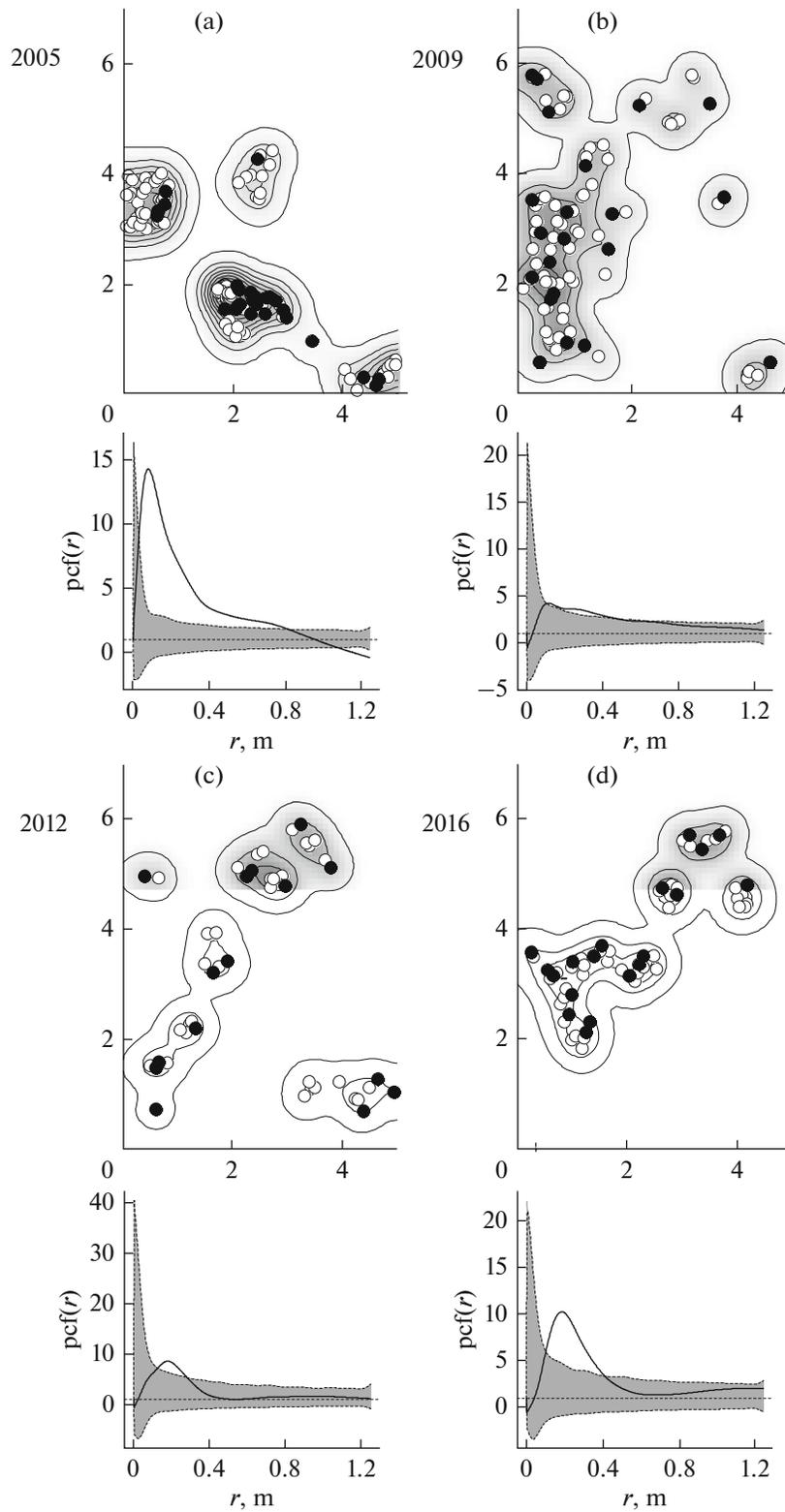
Fig. 4. Dynamics of the spatial structure of *N. cucullata* CP3: maps and pair correlation function. (a) 2005; (b) 2009; (c) 2012; and (d) 2016. Other indications correspond to those in Fig. 1.

Table 2. Correlation between the magnitude of *N. cucullata* population and climatic variables

Ontogenetic group	Precipitations	Air humidity	Number of days without precipitations	Temperature	$T \geq 30°C$	Number of sunny days
Juvenile	0.23	0.12	−0.34*	−0.33*	−0.28	−0.51*
Generative	0.66*	0.82*	−0.61*	−0.67*	−0.69*	0.16

* Statistically significant coefficients at the observed significance level $p < 0.05$.

N. cucullata was also observed on a bumpy area in the mossy pine forest with the rare species *Goodyera repens* (CP3, Table 1). After a small destruction of the habitat, the magnitude of the *N. cucullata* CP in 2005 was 110 with a density of 3.1 plant/m^2 (Fig. 4a). The population began to actively grow, and its magnitude increased to 8.1 in 2007; the population field was increased probably due to invasion processes and seeds, protocorms, and tubers hidden in the soil and mossy carpet (Fig. 4b). Though droughty summer periods (2009−2011) resulted in a sharp drop in population magnitude (only 62 plants in 2016), the age and spatial−age structures were not disturbed (Figs. 4c, 4d). The "captured" territory was occupied mainly by this species, and its population field remained more or less continual (see maps in Figs. 4c, 4d). The character of the spatial and ontogenetic structure remained discrete-continual (see the pair correlation function, Figs. 4c, 4d). The CP density slightly decreased to 2016, reaching 1.8 plants/m^2, and the size of aggregations also decreased from 0.8 to 0.4 m (Figs. 4c, 4d), but the age structure remained complete and was determined in a 3-m^2 elementary demographic unit. The correlation of the CP3 magnitude with climatic factors was similar to the same correlations for CP1 (Table 2).

The spatial contour dynamics and population field fragmentation probably take place due to the dynamics of a symbiotrophic fungi concentration influenced by the character of climatic conditions, especially precipitations; as a result, a sharp drop in reproduction occurs with the corresponding fluctuation of the number of orchids in different microloci. In general, though natural disasters worsen the state of populations, the process of population recovery is quite rapid, especially if the biotope was not disturbed and does not undergo a long-term anthropogenic impact.

Irreversible long-term population dynamics usually has a more complex character, which is determined not only by a complex of different environmental factors, but also by the duration and stability (frequency of changes) of their impact. Fluctuation dynamics of populations of meadow plant communities in the Middle Volga region is determined not only by the duration of the high-temperature period and the low amount of precipitation in summer, but also by the flooding regime of rivers and adjacent meadows and the groundwater level. Lowland meadows located in river valleys usually became waterlogged in the

beginning of June, but are completely dried off by the beginning of July. Let us consider the dynamics of the *Dactylorhiza incarnate* CP4 growing in the lowland meadows of the Kazanka River (central park of the city of Kazan) as an example of such irreversible spatial and temporal dynamics determined by zoogenic, phytogenic, and climatic factors (Table 1).

During the formation of the city park in the 1970s, a small drainage channel was formed. Numerous populations of *D. incarnata* growing together with *Orchis militaris* and *Ophiologlossum vulgatum* were observed in depressions located along this channel. Ornamental trees and shrubs were planted on mown meadows in the central part of the park. In the distant parts of the park, lowland meadows remained unchanged, but were periodically used for the pasturing of a small herd of cattle and goats that provided a thinned herbage required for the normal development of orchids (retardation subclimax, according to Razumovskii (1999)). From 1988 to 1996, the dynamics of *D. incarnata* CP4 consisted of fluctuations caused by different climatic conditions and periodical pasturing. Depending on the annual humidity, areas of the lowland meadow optimal for plant vegetation varied: during wet years, vegetating plants of the population were aggregated mainly in the higher central part of the meadow (Figs. 5b, 2001; 5c, 2006), while in droughty years they grew in depressions located along the channel (Fig. 5a, 1996).

However, such fluctuations of the population magnitude and spatial contour were also determined by other factors. From 1996 to 2009 (after pasture cessation on lowland meadows), the population dynamics became irreversible, which reflected the extinction of the *D. incarnata* population because of the interspecific competition with meadow grasses (Figs. 5a−5d). Demutation succession started on the meadows. Along with the grass density increase, willow bushes (*Salix acutifolia*, *S. triandra)*, which were earlier destroyed by goats, began to recover along the channel. A "dislocation" of the population field from the central part of the meadow to the path was observed on the studied area; this dislocation occurred along the gradient of increase of the anthropogenic disturbance and a soil humidity increase (Figs. 5c−5d, 2006, 2009). The spatial migration of CP4 was achieved due to juvenile plants. The population was invaded into the territory adjacent to the path, since moderate recreational activity suppress the overgrowth of bunchgrasses and, to some extent, provides
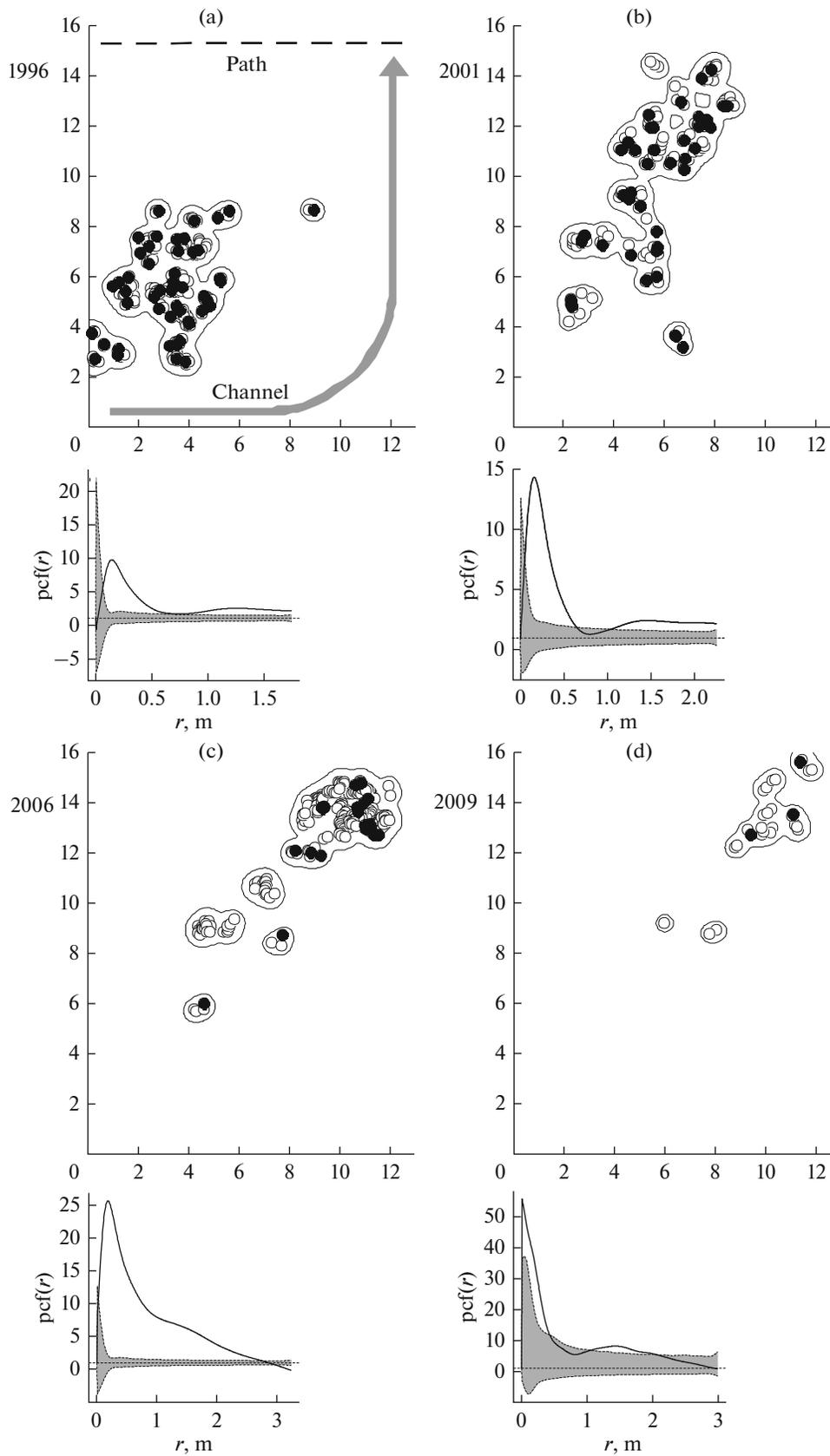
Fig. 5. Dynamics of the spatial structure of a *D. incarnata* coenopopulation: maps and pair correlation function. (a) 1996; (b) 2001; (c) 2006; and (d) 2009. Other indications correspond to those in Fig. 1. Because of the high population density, only one population density contour (1 plant/m^2) is shown.
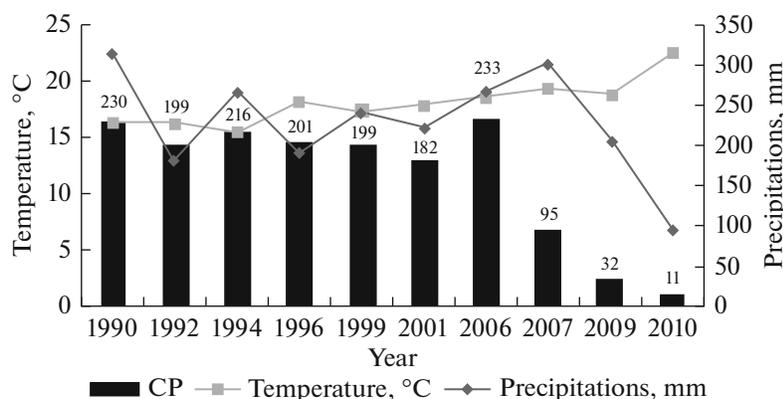
Fig. 6. Dynamics of the magnitude of a *D. incarnata* coenopopulation observed within 20 years.

weaker competition. Nevertheless, an increase in annual summer temperatures has been observed since the end of the 20th century, which resulted to the drought (2010) and the corresponding sharp reduction in the channel flooding and the formation of a grass meadow. The situation was aggravated due to the reconstruction of the park (2009), which resulted in the intensification of recreational activity. In 2012, the magnitude and density of *D. incarnata* reduced from 3.03 plant/m² (1988) to 0.13 plant/m² (2012, Fig. 6).

In the 10-year dynamics, a positive correlation was observed between the magnitude of the *D. incarnata* population and the amount of precipitations and air humidity; at the same time, a negative correlation of this parameter with high air temperatures and the number of sunny days was revealed (Table 3).

In general, conservative features of *D. incarnata* CP4, such as the ontogenetic spectrum and the character of its spatial and ontogenetic structure, did not significantly change within 10 years of observations. The ontogenetic spectrum remained left-handed with the predomination of juvenile plants, the percentage of which varied within 55−85%. The spatial pattern of arrangement of juvenile plants can be classified as discrete-continual (Fardeeva, 2016); it was observed during the whole monitoring period and included multiply aged frequently repeated monocentric aggregations with a radius of 0.4−0.6 m and a distance between their centers of 1.2−1.4 m; these aggregations formed the larger second-order aggregations. An intensive meadow-recovering succession occurring in the studied habitat caused the initial general depopulation; the further sharp drop in the population mag-

nitude caused by the drought and intensifying recreational load resulted in the disturbance of the complete cycle of generations. The state of the population is determined as critical, so it may become extinct in the course of further grass recovery.

Anomalous climatic conditions (such as the drought) and the intensification of anthropogenic impact result in significant successions of natural population complexes that influence on the state of populations of rare species. However, the dynamics of communities and populations has a cyclic character; in the case of the minimization of the anthropogenic impact, the state of phytocoenosis and a rare species population may return to the initial type. In general, these regularities may appear at any hierarchical population level, from microloci and coenopopulations to the species populations in a regional scale or within the occupied habitat.

CONCLUSIONS

The fluctuation dynamics of a spatial and ontogenetic structure of populations of tuberous orchids is determined by the sum of different factors, including weather conditions and phytogenic, zoogenic, and anthropogenic impacts of different characters and durations. One important factor for tuberous orchid populations is the maintenance or appearance (due to endogenous or exogenous factors) of ecological space with a weakened interspecific competition processes, which appear in the case of insignificant and often indirect weather, as well as anthropogenic, zoogenic, or phytogenic impacts, and provide a dynamic equi-

Table 3. Correlation between the magnitude of *D. incarnata* population and climatic variables

Ontogenetic group	Precipitations	Air humidity	Number of sunny days	Temperature
Juvenile	0.60*	0.80*	−0.54*	−0.71*
Generative	0.38*	0.82*	−0.77*	−0.76*

*Statistically significant coefficients at the observed significance level $p < 0.05$.

librium. The stability is determined by high seed productivity and the activation of migration processes via invasion into more favorable microhabitats.

In general, populations of tuberous orchids are characterized by a noticeable and active fluctuation dynamics. The shorter the duration of ontogenetic periods (especially generative plants) and ontogenesis as a whole and the lower the ability to rejuvenate due to vegetative clones (or the higher the ability to rejuvenate due to seed vegetation), the more dynamic the spatial and temporal structure of the population is. Single or minimal anthropogenic impacts result in some changes in the magnitude, density, and spatial contour of a population, but later these parameters recover back to their initial values. Irreversible changes in orchid populations may be caused by either digression and dimutation processes occurring in phytocoenoses, or disaster factors, including anthropogenic impact. However, the successions of plant communities often result in the extinction of orchid populations.

For tuberous orchid species, the dynamics of their spatial pattern, accompanied by migrations of orchid plants towards more favorable microsites, is a natural compensatory mechanism of stability providing the dynamic equilibrium of their populations.

COMPLIANCE WITH ETHICAL STANDARDS

The authors declare that they have no conflict of interest. This article does not contain any studies involving animals or human participants performed by any of the authors.

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