Current Research in Environmental & Applied Mycology (Journal of Fungal Biology)
11(1): 468–484 (2021) ISSN 2229-2225
www.creamjournal.org

Article

Doi 10.5943/cream/11/1/32

Distribution and ecological niche modeling of a rare species *Poronia punctata* in Asia

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Vlasenko VA, Dejidmaa T, Dondov B, Ochirbat E, Kherlenchimeg N, Javkhlan S, Burenbaatar G, Uranchimeg A, Asbaganov SV, Vlasenko AV 2021 – Distribution and ecological niche modeling of a rare species *Poronia punctata* in Asia. Current Research in Environmental & Applied Mycology (Journal of Fungal Biology) 11(1), 468–484, Doi 10.5943/cream/11/1/32

Abstract

The ability to identify the spatial distribution of rare fungal species is crucial for the understanding of the environmental factors that affect them and their conservation management. Maximum entropy spatial distribution modelling (MaxEnt) solves this problem by inferring species distributions and environmental tolerance based on the occurrence data. We constructed a map of the current and potential geographical distribution of the dung fungus *Poronia punctata* using this method. We included in the model 19 WorldClim bioclimatic variables with the corresponding altitude data, and 23 spatially well-dispersed species occurrence records. We defined the regularities in spatial distribution of *P*. *punctata* based on the occurrence data, as well as bioclimatic characteristics in order to control species status in the natural environment. The majority of the locations of *P*. *punctata* in Asia are placed in the middle mountains. In addition to the presence of a suitable substrate and the habitat type, the geographical distribution of *P*. *punctata* depends on a set of environmental factors that are optimal for this species. Optimal climatic conditions for *P*. *punctata* in Asia are typical for steppe communities and steppe shrub thickets of intermontane depressions of Lakes Basins and lowlands between mountain ranges. All species habitats were associated to the vegetation type of steppe and forest-steppe. Locations within the boundaries of Temperate Coniferous and Boreal Forest occurred in the habitats affected by anthropogenic activity and grazing, subjected to steppe formation; these locations were confined to river valleys and lakes, which also brings them closer to the habitats of depressions and lowlands. The points of presence occurring in intermontane depressions and lowlands between mountain ranges represent the environment core of *P*. *punctata* range in Asia.

Keywords – distribution – dung fungi – ecological niche – Inner Asia – mountainous area

Introduction

Fungal and plant species distribution is undergoing rapid changes in the face of habitat

Submitted 24 June 2021, Accepted 19 October 2021, Published 3 December 2021
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modification and climate change. This leads to concerns about the conservation of declining species and raises ecological questions about the processes that governs species ranges and niches. As a consequence, the predictive distribution models which match species records to patterns in abiotic environmental variables have become an established tool in ecology and conservation (Segurado & Araújo 2004, Guisan & Thuiller 2005, Elith et al. 2006, Hickling et al. 2006, La Sorte & Thompson 2007, Lenoir et al. 2008, Chapman & Purse 2011).

Species distribution models (SDMs) constitute the most common class of models in ecology, evolution and conservation. The new software packages and the increasing availability of digital GIS have greatly facilitated the use of SDMs (Zurell et al. 2020).

Species distribution models are empirical models connecting field observations to environmental predictor variables based on statistically or theoretically derived response surfaces (Guisan & Zimmermann 2000). Environmental predictors can exert direct or indirect effects on species, thus forming a gradient from proximal to distal predictors (Austin 2002).

There is some of the potentials for using SDMs in ecology: quantifying the environmental niche (Austin 1990, Vetaas 2002); assessing species invasion (Beerling et al. 1995, Peterson 2003); assessing the impact of climate changes on species distribution (Thomas et al. 2004, Thuiller 2004); modelling of species biodiversity based on the individual species predictions (Leathwick et al. 1996, Guisan & Theurillat 2000, Ferrier et al. 2002, Guisan & Thuiller 2005).

MaxEnt is one of the most commonly used methods for inferring species distributions and environmental tolerances from occurrence data (Phillips & Dudík 2008). MaxEnt uses the principle of maximum entropy based on presence-only data to estimate a set of functions that connect environmental variables and habitat suitability in order to approximate species niche and potential geographic distribution (Phillips et al. 2006).

Environmental (or ecological) niche model (ENM) is a model that uses occurrence data in conjunction with environmental data to create a correlative model of the environmental conditions that meet species ecological requirements and predict the relative suitability of a habitat. ENMs are most often used in one of the following cases: (1) to estimate the relative suitability of a habitat known to be occupied by a species, (2) to estimate the relative suitability of a habitat in a geographic area that is not known to be occupied by a species, (3) to estimate changes in the suitability of a habitat over period of time given a specific scenario for the environmental change, and (4) to estimate species niche (Warren & Seifert 2011).

Distribution and niche modeling is usually carried out for species interesting for conservation (Wright & Westerhoff 2001). In addition, researchers tend to record locations of rare species more accurately and therefore attract particular attention to the records. Endangered and vulnerable species, especially the highly specialised ones, may be more sensitive to environmental changes. Many studies have suggested that species with restricted ecological niches can be modelled with greater accuracy than the more generalist ones (Hepinstall et al. 2002, Brotons et al. 2004, Hernandez et al. 2006, Tsoar et al. 2007).

Species that are more common should not be overlooked though, as they could also become rare or suffer a future decline because of environmental changes; they may also have significant roles for ecosystems' structure and functioning (Gaston & Fuller 2007).

MaxEnt modeling has recently become an actively used tool for fungi. For example, it is used to identify the spatial distribution of economically important fungal species in order to understand the environmental factors that affect them and for their conservation management (Yuan et al. 2015, Guo et al. 2017, Pietras et al. 2018).

Poronia punctata (L.) Fr. is a dung fungus. Dung fungi are species that live on or are associated with animal dung or dung-amended soil. Most of them have been found on dung of warm-blooded animals (Krug et al. 2004), primarily herbivores (Dix & Webster 1995, Krug et al. 2004).

The rarity of *P. punctata* is controversial. Even Whalley & Dickson (1986) wondered whether this species is really declining or remains overlooked, due to the peculiarities of its ecology. The number entries for the species worldwide reaches 1260. Based on species classification using the occurrence frequency, we classify *P. punctata* as a common species. The IUCN Red List attributes this species the LC (Least Concern) class (Persiani & Ainsworth 2020).

Poronia punctata, like others dung fungi represent an astonishing example of specialised microorganisms, perfectly adapted to the complex and extreme substrate. Their specialisation involves specific mechanisms: spores survive digestion, passage through the animal digestive tract activate spores, and fungi have special nutritional requirements and adaptations to specific physicochemical conditions of the dung. Dung represents a complex rich substrate, providing a wide range of nutrients (readily available carbohydrates, cellulose, lignin, high nitrogen content, water, growth factors, minerals) as well as microhabitats (Dix & Webster 1995, Richardson 2001).

Dung fungi, including *Poronia punctata*, are important in contexts of biodiversity, ecology, paleoecology and biotechnology, and are worth protection (Fernandez et al. 2020). They provide fundamental ecological services, playing pivotal roles in dung decomposition, soil formation and stabilisation, as well as biogeochemical cycling of nutrients and elements (Dix & Webster 1995, Barron 2017). They represent model objects for research in ecology and biodiversity (Krug et al. 2004).

Douglas (2009) has previously conducted the habitat suitability modeling for *P. punctata* in New Forest National Park in United Kingdom only. In Asia, there was no previously conducted spatial distribution and habitat suitability modelling for *P. punctata*.

The objectives of this research were establishing the spatial distribution pattern, running the habitat suitability modelling and estimating the potential effects of climate change on dung fungal species *P. punctata* based on its bioclimatic and substrate features within Asia.

Materials & Methods

Object of study (Taxa)

The *Poronia* genus contains approximately nine species. *Poronia punctata* (L.) Fr. is a fungus from the Xylariaceae family, growing on dung (Fig. 1).

This species has a characteristic peg top shaped stromata with a whitish disk-like upper surface, mounted upon an unbranched stalk, rarely more than 1 cm height (in nature). In the earlier stages of its development, the upper parts of the stromata are covered with greyish white powder, the conidia. Black spots scattered over the flat surface of the disk follow these. Mentioned spots are the perithecia ostioles, which are embedded in the uppermost layers of the stromata. When the asci are quite ripe they protrude minute black pillar-like masses enclosing numerous ascospores above the surface. The asci are club-shaped and enclose eight dark brown ascospores, ellipsoidal in form and having a lateral slit-like pit in the outer wall. Amongst the asci, there are numerous colourless, long, slender, multicellular paraphyses. Conidia are small colourless pear-shaped bodies, with oil-like drops, and are formed by the abstriction of the tips of terminal stroma hyphae. In some cases, the stromata do not expand above into a disk-shaped formation, but remains the column shape, in which case only conidia form, and there is no trace of perithecia (Dawson 1900, Whalley & Dickson 1986).

Poronia punctata is widespread in Eurasia, North America, and Australia; also, there are records in South America and Africa.

Typical habitats of this species are artificial terrestrial shrubland and grassland (according to the habitat classification system of IUCN). Threats to this species existence are the reduction of the cattle numbers and the changes in natural environment. According to the IUCN Red List *P. punctata* requires a research to identify its distribution and habitat trends, in order to control its condition in natural environment https://www.iucnredlist.org/species/58517228/185715679.

Field studies

We obtained data on the distribution of the studied fungal species based on the fruiting bodies collected by us during 2008–2020 expeditions. We carried out our fieldwork in the south of Western Siberia (Northern Asia): on the plains of Novosibirsk Region (in 2014, 2016), Omsk

Region (2016), the Altai Territory (2015, 2018, 2019), as well as in the mountainous regions of Inner Asia: in Republic of Altai (2008, 2019, 2020), Republic of Tuva (2020) and Mongolia (2019).

Fig. 1 – Stromata of *Poronia punctata* on horse dung. A *P. punctata* from Republic of Altai, Loc. 9. B *P. punctata* from Republic of Tuva, Loc. 17.

Morphological examination

We performed the initial morphological examination of *P. punctata* fruiting bodies using Carl Zeiss Stemi DV4 stereomicroscope, Carl Zeiss Axiolab E light microscope and Carl Zeiss Axioskop-40 light microscope.

Biodiversity data overview and Study area

This research includes materials collected during our expeditions. Voucher specimens of the studied species are stored in the MG Popov Herbarium (NSK), Novosibirsk, Russia.

We used records supported by specific geographic coordinates only. In total, we included 23 locations of *P. punctata* in Asia, of which seven we established ourselves for the first time (samples with NSK numbers). Fig. 2 shows the locations used in the distribution and niche modeling analysis within Asian boundaries, description is given in Table 1. The samples deposited in the NSK herbarium were collected by V.A. and A.V. Vlasenko.

SDM algorithms, predictor type, software and data used

When creating the distribution model for *P. punctata*, we used a protocol that is close in basic parameters to ODMAP (Zurell et al. 2020).

We used the computer program DIVA-GIS (Hijmans et al. 2012) for mapping and geographic data analysis (https://www.diva-gis.org/). We downloaded data on the relief and the heights of the studied locations, as well as global data on current (~1950–2000) and future (2xCO_2 climate conditions, CCM_3 model, 2100 AD) climates from https://www.diva-gis.org/Data and https://www.diva-gis.org/climate, source Worldclim, version 1.3.

We obtained the global country boundaries (WGS84) https://hub.arcgis.com/datasets/a21fdb46d23e4ef896f31475217cbb08_1/data?geometry=-99.844%2C-89.998%2C99.844%2C-79.394.

All the 19 environmental layers of Bioclim (BIO1-BIO19) constructed using the DIVA-GIS with 2.5-minute resolution (30 arc seconds square) encompassed most of the Asian subcontinent (Hijmans et al. 2005).

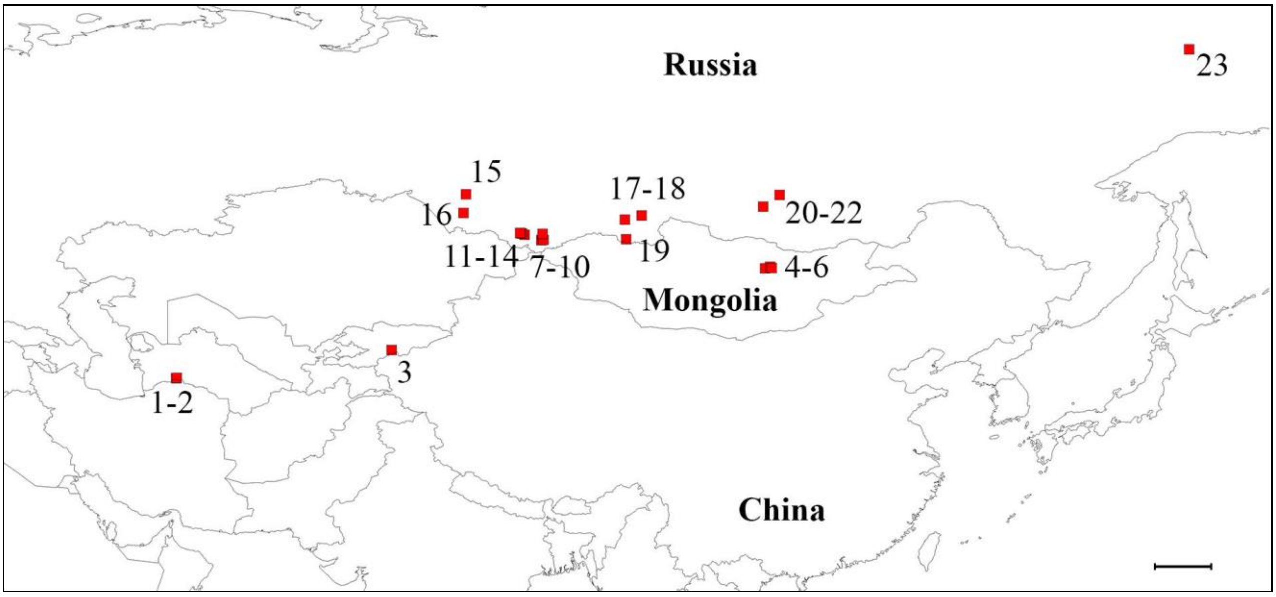

Fig. 2 – Locations of *Poronia punctata* in Asia. Scale bar = 500 km.

Table 1 Locations of *Poronia punctata* in Asia.

Country, area	Locality	Region	Coordinates	Data source
Turkmenistan, Kopet Dag Mts.	Loc. 1	Balkan Region, Tutlycala	38.3930°N, 56.7240°E, 1052 m	Internet data
	Loc. 2	Ibid.	38.4175°N, 56.7803°E, 911 m	Internet data
Kyrgyzstan, Tian Shan Mts.	Loc. 3	Naryn Province, At-Bashi District, Chatyr-Kul	40.7900°N, 75.1091°E, 3252 m	Internet data
Mongolia, Khentii Mts.	Loc. 4	Töv Province, Bogd Khan Mt, Manjusri Monastery	47.7649°N, 106.9955°E, 1797 m	Internet data
	Loc. 5	Gorkhi-Terelj National Park, Turtle Mt.	47.9050°N, 107.4259°E, 1524 m	Internet data
	Loc. 6	Gorkhi-Terelj National Park, Terelj	47.9500°N, 107.5702°E, 1488 m	Internet data
Russia, Altai Mts.	Loc. 7	Republic of Altai, Kosh-Agachsky district, Kyzyl-Tash, Tyute River, Kurai steppe	50.1706°N, 87.8971°E, 1529 m	Internet data
	Loc. 8	Ibid., Kyzyl-Tash, Chuya River, Kurai steppe	50.1829°N, 87.9923°E, 1518 m	NSK 1014784
	Loc. 9	Ibid.	50.1914°N, 88.0876°E, 1599 m	NSK 1014783
	Loc. 10	Ibid., Ulagan District, Balyktuyul	50.7026°N, 88.0165°E, 1260 m	Internet data
	Loc. 11	Ibid., Ongudai District, Kupchegen	50.6126°N, 86.4700°E, 773 m	NSK 1014785
	Loc. 12	Ibid., Ongudai	50.7261°N, 86.2468°E, 779 m	NSK 1014786
	Loc. 13	Ibid.	50.7639°N, 86.1076°E, 850 m	NSK 1014787
	Loc. 14	Ibid.	50.7790°N, 86.0810°E, 869 m	NSK 1014788
Western Siberia, forest-steppe zone	Loc. 15	Novosibirsk Region, Ordynsky district, mouth of the Aleus River, the coast of the Ob Reservoir	54.0943°N, 81.4589°E, 127 m	Gorbunova (2006)

Table 1 Continued.

Country, area	Locality	Region	Coordinates	Data source
Western Siberia, steppe zone	Loc. 16	Altai Territory, Romanovsky District, Gorkoye Lake	52.4762°N, 81.2567°E, 199 m	Gorbunova & Perova (2006)
Eastern Siberia	Loc. 17	Republic of Tuva, Kyzylsky District, Tapsinskiy Nature Preserve	51.9322°N, 95.0438°E, 1122 m	NSK 1014661
Eastern Siberia, Sayan Mts.	Loc. 18	Ibid., Todzhinskiy District, Todzha	52.2697°N, 96.4619°E, 998 m	Internet data
Eastern Siberia, Tannu-Ola Mts.	Loc. 19	Ibid., Erzinsky District, Erzin	50.2591°N, 95.1530°E, 1100 m	Internet data
Eastern Siberia, Baikal region	Loc. 20	Irkutsk Region, Olkhonsky District, Kurkut	53.0291°N, 106.8515°E, 534 m	Internet data
	Loc. 21	Ibid.	53.0292°N, 106.8402°E, 482	Internet data
	Loc. 22	Ibid., cape Pokoyniki	54.0160°N, 108.2395°E, 468 m	Gorbunova & Stepantsova (2015)
Eastern Siberia	Loc. 23	Republic of Sakha (Yakutia), Moma District, Honuu	66.4550°N, 143.2187°E, 191 m	Internet data

We downloaded data on the Biomes, Terrestrial Ecoregions of the World (Olson et al. 2001), from https://www.worldwildlife.org/publications/terrestrial-ecoregions-of-the-world, and from https://www.arcgis.com/apps/View/index.html?appid=d60ec415febb4874ac5e0960a6a2e448.

We constructed the climatic profile of *P. punctata* using the BIOCLIM method. This method developed by Nix (1986) constructs histograms of bioclimatic variables that reflect species climate profile. The DIVA-GIS software implements the BIOCLIM method.

We used MaxEnt (Phillips & Dudík 2008) to conduct species habitat suitability modelling. MaxEnt employs a maximum entropy modelling approach by using inputs of environmental variables and species occurrence data to create a predictive model of habitat suitability for a given species. Once a model describing conditions suitable for a species is built based on species presence and environmental data, MaxEnt can use a combination of constant and changing environmental conditions to predict probabilities of species occurrence under a variety of future scenarios. Spatial distribution pattern for *P. punctata* using the maximum entropy method (MaxEnt) based on a 23-point dataset.

We used DIVA-GIS and MaxEnt programs in accordance with the recommendations from the manual on spatial analysis of plant diversity and distribution (Scheldeman & Zonneveld 2010).

Results & Discussion

Biology and life cycle attributes, as well as the availability of a suitable substrate, habitats and environmental factors limit the distribution of fungal species. The developmental biology of *P. punctata* has been studied since the early 20th century. The studies were carried out for pure cultures grown on 10% gelatinous media with horse dung decoction and later transferred from agar to cotton wool, where they began to grow and generate stromata. Fruiting bodies grew more rapidly at temperatures ranging from10°C–13°C than 15°C–18°C (Dawson 1900).

Modern research into the biology of this species belongs to the beginning of the 21st century. Studies investigated the environmental conditions of fruiting (e.g. temperature, water content, nutrients), as well as substrate (dung) and habitat the features (Bignell & King 2011, Edwards 2015, Matočec 2000).

Edwards et al. (2015) assumed that like many other dung fungi, ascospores of *P. punctata* germinate only after passing through the digestive tract of herbivores.

Initially, Dawson (1900) believed that *P. punctata* develops only on horse dung. Probably, the fungus utilises cellulose or some product of its fermentation. Later, this species was also found on cow (Matočec 2000, Minter 2006, Bignell & King 2011, Edwards 2015), sheep and elephant (Szczepkowski & Obidziński 2016) dung. In Asia, *P. punctata* was recorded only on horse dung. *P. punctata* has a complex life cycle, which includes an anamorphic phase (Edwards et al. 2015, Granito & Lunghini 2006, Stiers et al. 1973).

Previously Douglas (2009) carried out the habitat suitability modeling for *P. punctata* in the New Forest National Park in United Kingdom using Biomapper habitat suitability maps. The study found that *P. punctata* tends to occupy sites with higher percentage of dry heath cover or similar habitat types. In these habitats, a greater cover of grass for grazing is more likely to occur. *P. punctata* also showed preference for the sites that receive higher precipitation in July. This may reflect a need of some excessive moisture leading up to the fruit body formation (generally from early autumn). Studies also show that many records of the fungus came from the places with shrubs. The used approach does not require GIS data but Bayesian Belief Network (BBN) based on literature data. The method estimated the impact of the selected variables on climate change. Habitat suitability modeling by BBN showed that all-natural habitats with present manure are suitable for the species. Moreover, variables such as Ground moisture, Ground vegetation height, Tree canopy cover, soil type and habitat type have very little or no effect.

Multiple-factor interactions are essential for fungal fruiting, that includes type and height of vegetation, which creates favourable microclimatic conditions, as well as the presence of insects (especially dung beetles) which improves the rate of dung decay and aeration and supports fungal growth and reproduction (Edwards 2015).

In our study, we made all the records in the steppe communities of Altai and Tuva. Fig. 3 shows the typical habitats.

Fig 3 – Typical habitats of *P. punctata*. A Republic of Altai, Kurai depression, Loc 9, steppe. B Republic of Tuva, Loc 17, steppe meadow.

According to the data from The Global Fungal Red List Initiative, *P. punctata* has had a significant decline compared to its historic levels, and is now considered rare in most of its range. This decline has largely occurred during the twentieth century, differing in timing throughout its range depending on when the shift from horse-powered to mechanical transport agriculture occurred. In some countries (e.g. Austria and Finland), it is now extinct. However, the total population is now thought to be stable and perhaps increasing in some parts of Europe (e.g. UK and parts of Sweden) and elsewhere, as people increasingly use horses for conservation management purposes http://iucn.ekoo.se/iucn/species_view/198420/.

In Europe, authors observed and studied *P. punctata*, reporting on important findings on its biology and conservation (Bignell & King 2011, Cox et al. 2005, Edwards 2015, Edwards et al.

2015). Many European countries proposed or included *P. punctata* in National Red Lists (Gyosheva et al. 2006, Kajevska et al. 2019, Karadelev & Rusevska 2016, Koszka 2008, Mirek et al. 2006, Rossi et al. 2013, Szczepkowski & Obidziński 2016).

All the records of *P. punctata* in Asia came from steppes or from steppe territories modified in the course of anthropogenic activities and used for grazing. The steppe is a typical habitat of the fungus and contains a suitable substrate for the species as cattle graze there. However, for more than 100 year of mycological research this species appeared only twice in the steppes of the flat territory of the Asian subcontinent, the south of Western Siberia: in the steppe zone of the Altai Territory and in the forest-steppe zone of the Novosibirsk Region. The species occurred mainly in mountainous regions. Apparently, an established spectrum of specific bioclimatic and other factors is required for *P. punctata* development, in addition to the specific biology, life cycle features and the availability of a suitable substrate and habitat type.

Climatic niche modeling for P. punctata

The climatic niche of a species bases on the identification of the climatic characteristics of the locations where the studied species appeared. It should be noted that the climatic data obtained by meteorological stations and extrapolated to large areas, reflect only general trends in the influence of the main environmental factors and do not account the characteristics of individual habitats (Scheldeman & Zonneveld 2010).

The species climatic niche was constructed using the BIOCLIM method. This method gives reliable results when modeling the habitat of large areas, and not for the local habitat.

In the distribution model for *P. punctata* built in MaxEnt the bioclimatic variables that most strongly affected species distribution are BIO15 (Precipitation Seasonality (Coefficient of Variation)), BIO16 (Precipitation of Wettest Quarter), BIO 3 (Isothermality (BIO1/BIO7) * 100), and BIO14 (Precipitation of Driest Period). We removed a duplicate presence point within the same cell in the climate raster (in Baikal Region). As a result, the analysis included 22 points of presence.

We generated the frequency histograms based on the most significant bioclimatic variables for *P. punctata* in MaxEnt analysis as well as for BIO1 (Annual Mean Temperature) and BIO12 (Annual Precipitation) (Fig. 4) regardless of their contribution to the model. The histograms show the distribution of *P. punctata* along the customized ranges for different climatic variables.

We carried out the modeling of a two-dimensional niche for *P. punctata* using two bioclimatic variables – Annual Mean Temperature and Annual Precipitation (Fig. 5).

We adjusted the width of the niche by changing the percentile values. We narrowed the niche to define the environment core of the species range. We changed the limits of the two-dimensional niche within 0.000 – 0.025 – 0.050 – 0.100 (100% – 95% – 90% – 80% of the presence points were used in developing the two-dimensional niche, respectively). Fig 6 presents the result of determining the environment core of the species range.

The constructed model showed that the points of presence occurring in intermontane depressions and lowlands between mountain ranges represent the environment core of *P. punctata* range in Asia. These areas contain steppe communities that are located in Tian Shan Mts., Altai Mts., Hentey Mts., Great Lakes Basin (Uvs Nuur Basin), Baykal Mts. (coasts of Baykal Like). On the flat territory of Western Siberia, the ecological core of the species includes a point in the Novosibirsk Region on a bank of the Ob reservoir.

Distribution modeling for P. punctata in relation to the relief elevation

Within the latitudinal gradient, the distribution of *P. punctata* in Asia lays between the 38th parallel in the South and the 67th parallel in the North. Locations of *P. punctata* in Asia are distributed from southwest to northeast from the extreme point in the Kopet Dag Mts., through Tian Shan Mts., Altay Mts., Sayan Mts., Baykal Mts., and Southwest Spurs of Khentei in Mongolia up to the mountain ranges of Yakutia. Locations of *P. punctata* on a relief basis are shown in Fig. 7.

The majority of the locations of *P. punctata* in Asia are placed in the middle mountains with heights between 800-2000 m ASL: Kopet Dag Mts. (911-1052 m), Sayan Mts. (998-1122 m), Altay

Mts. (Central Altai 773-869 m; Eastern Altai 1260 m; Southeast Altai 1518-1599 m), Hentey Mts. (1488-1797 m).

Potential distribution modeling for P. punctata in current climate

The MaxEnt models we obtained have high Area Under Receiver Operating Characteristic Curve (AUC) value: 0.965. To evaluate the model, we used a test sample that included 25% of all points of presence. The AUC value for the test data was 0.910. Both AUC values fall within the range of 0.9–1, thus corresponding to the excellent discrimination (Scheldeman & Zonneveld 2010).

In analysis, we used the 10-percentile training threshold for the presence, found in the table of thresholds generated by MaxEnt. The threshold value for *P. punctata* is 0.121 (Table 2). Fig. 8 represents the potential species distribution map and shows the area bounded by the 10% presence threshold in blue.

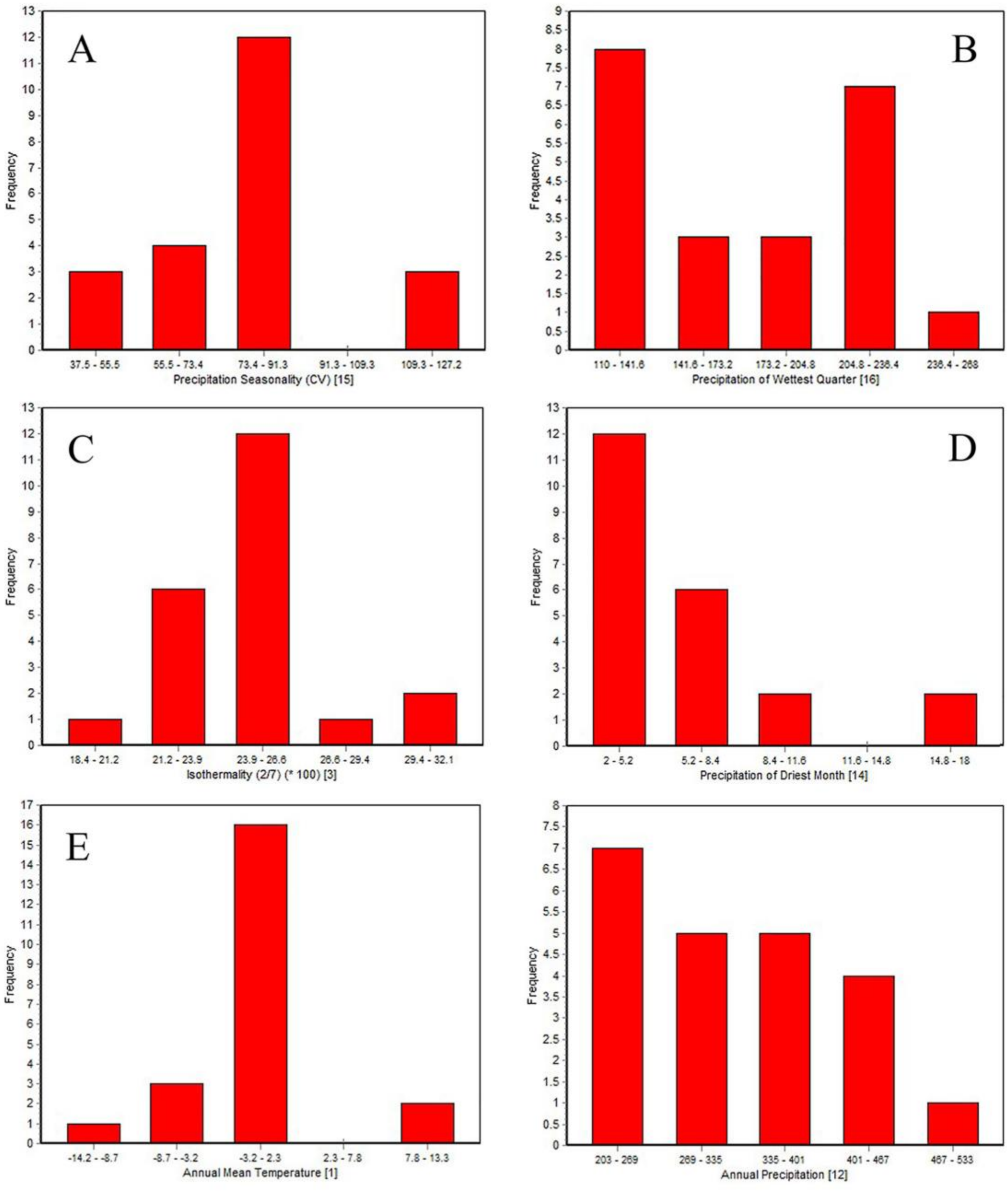

Fig. 4 – Frequency histograms, which show the distribution of *P. punctata* along customized ranges. A Precipitation Seasonality (Coefficient of Variation) BIO15, B Precipitation of Wettest Quarter BIO16, C Isothermality BIO3, D Precipitation of Driest Period BIO14, E Annual Mean

Temperature BIO1, F Annual Precipitation BIO12. Axis of abscissa – the factor strength, ordinate axis – the frequencies.

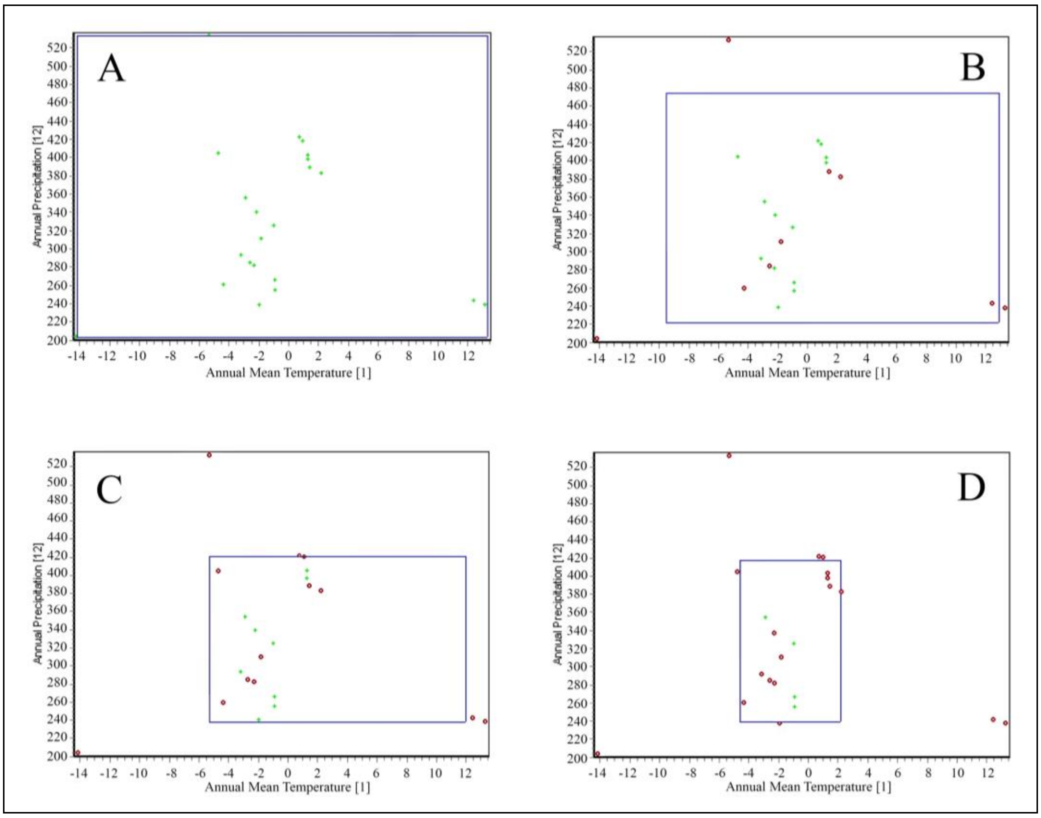

Fig. 5 – Visualization of a two-dimensional niche for *P. punctata* based on two climatic variables using the Envelope method. Limits of the two-dimensional niche: A 0.000, B 0.025, C 0.050, D 0.100. Blue rectangle is the climatic niche. The green points represent the presence points with a climate profile within the range limits of all the 19 Bioclim climatic variables. Red points outside the blue rectangles represent presence points with a climate profile with one or more values laying outside the range limits of the 19 Bioclim climatic variables. Red points within the blue rectangle represent presence points with a climate profile within the values of the range limits for the selected variables (Annual Mean Temperature and Annual Precipitation), but with one or more values laying outside the range limits of the other 17 Bioclim variables.

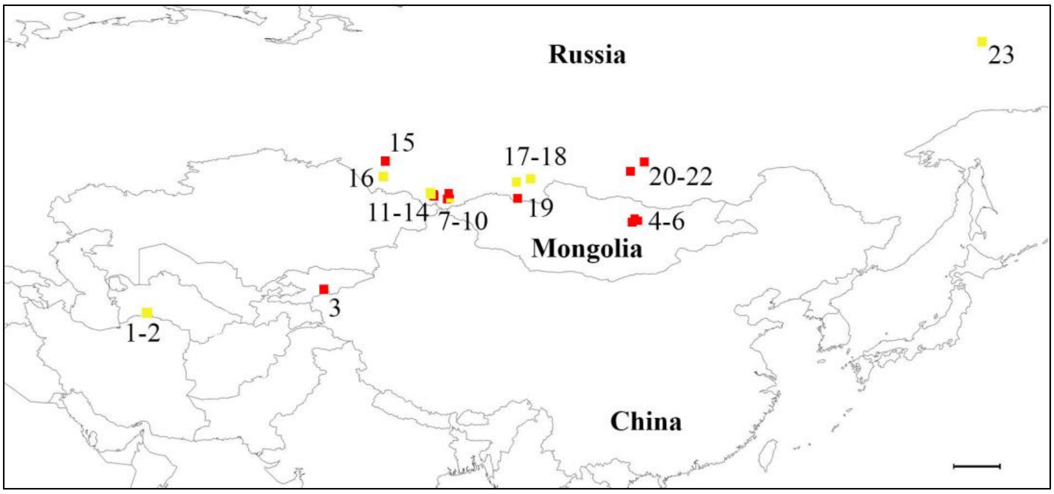

Fig. 6 – Model of the environment core (red points) of *P. punctata* range with the niche width limit of the two-dimensional niche = 0.100.

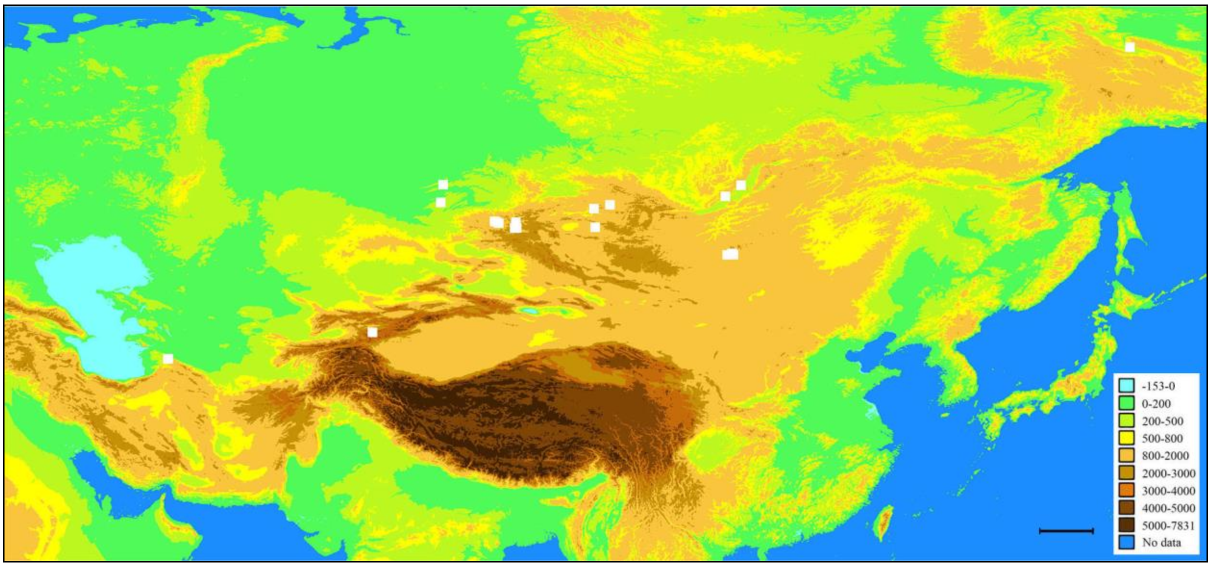

Fig. 7 – Distribution of *P. punctata* in Asia and its relation to the relief of the area. The legend shows a scale of heights, from min to max in meters above sea level. Gradation of heights = 0-200 m – lowland, 200-500 m – upland, 500-800 m – low mountains, 800-2000 m – middle mountains, more than 2000 m – highlands.

Table 2 Common thresholds and the corresponding omission rates (Current climate)

Cumulative threshold	Logistic threshold	Description	Fractional predicted area	Training omission rate
1.000	0.014	Fixed cumulative value 1	0.572	0.000
5.000	0.056	Fixed cumulative value 5	0.358	0.000
10.000	0.095	Fixed cumulative value 10	0.255	0.000
17.495	0.155	Minimum training presence	0.167	0.000
23.437	0.199	**10 percentile training presence**	**0.121**	0.091
23.452	0.199	Equal training sensitivity and specificity	0.121	0.136
17.495	0.155	Maximum training sensitivity plus specificity	0.167	0.000
5.795	0.062	Balance training omission, predicted area and threshold value	0.337	0.000
17.832	0.157	Equate entropy of thresholded and original distributions	0.164	0.045

MaxEnt analysis showed several areas with climatic conditions similar to the revealed niche of *P. punctata* in current climate.

In the constructed model, the locations in the lowlands at altitudes less than 200 m ASL located in the area with the lowest probability of the species presence: Yakutia (Loc 23) 0.121-0.15; the Altai Territory and the Novosibirsk Region (Loc 15, 16) 0.15-0.23. In addition, a location in Tuva was included in this category (Loc 17), located in the middle mountains.

Findings of *P. punctata* in lowlands at altitudes less than 200 m ASL belong to Yakutia steppe habitats, with grazing areas near settlements. Findings of *P. punctata* in the south of the West Siberian Plain belong to the steppe zone of the Altai Territory (199 m ASL, in the steppe near a lake) and to the forest-steppe zone of the Novosibirsk Region (127 m ASL, in a steppe meadow habitat, on a bank of the Ob reservoir).

In Baykal Mts., *P. punctata* occurred in steppe forests on the coasts of Baykal Lake (at heights of 468-534 m ASL, correlated with the lake height of 456 m ASL). As shown by the MaxEnt model and the distribution analysis in relation to topography, the coasts of Lake Baykal are favourable for the development of the species.

In most of the identified locations, the probability of the presence of the species was 0.31-0.77; these locations are present in the middle and high mountains.

Isolated findings of *P. punctata* in Asia belong to the highlands with heights exceeding 2000 m ASL: The Tian Shan Mts. (3252 m). This height limitation is likely to reflect the spread of equids (Perissodactyla).

Everywhere in the mountain areas (Kopet Dag Mts. Altay Mts., Sayan Mts., and Southwestern spurs of Hentey Mts. in Mongolia), the species occurs in the intermontane basins (Kurai steppe in Altay), Great Lakes Basin (Uvs Nuur Basin in Tuva) and lowlands between mountain ranges where the steppe is present.

Potential distribution modeling for P. punctata in future climate

The maximum entropy models we obtained have high Area Under Receiver Operating Characteristic Curve (AUC) value: 0.966. To evaluate the model, we used a test sample that included 25% of all points of presence. The AUC value for the test data was 0.910.

In the analysis, we used the 10-percentile training presence threshold, found in the table of thresholds generated by MaxEnt. The threshold value for *P. punctata* is 0.124 (Table 3). Fig. 9 shows the area of the potential distribution map bounded by the 10% presence threshold in blue.

Table 3 Common thresholds and the corresponding omission rates (Future climate)

Cumulative threshold	Logistic threshold	Description	Fractional predicted area	Training omission rate
1.000	0.014	Fixed cumulative value 1	0.497	0.000
5.000	0.059	Fixed cumulative value 5	0.302	0.000
10.000	0.113	Fixed cumulative value 10	0.214	0.000
13.328	0.147	Minimum training presence	0.179	0.000
21.025	0.224	**10 percentile training presence**	**0.124**	0.091
21.025	0.224	Equal training sensitivity and specificity	0.124	0.136
20.845	0.222	Maximum training sensitivity plus specificity	0.125	0.045
5.072	0.060	Balance training omission, predicted area and threshold value	0.300	0.000
15.609	0.171	Equate entropy of thresholded and original distributions	0.159	0.045

MaxEnt analysis showed several areas with climatic conditions similar to the revealed *P. punctata* niche in future climate.

We projected the future distributions of *P. punctata* in 2100 AD under the 2xCO_2 climate conditions CCM_3 model. The model simulations indicated that the area of marginally suitable habitats would undergo a relatively small change under the given scenario; however, the suitable habitats would decrease. Conditions in the areas where the species occurs now with the heights under 200m ASL: flat territories in the south of Western Siberia in the steppe of Altai territory and the forest-steppe of the Novosibirsk Region, would be more favorable. The most suitable habitats for the species located in mountainous regions will remain so in the future. The species model distribution constructed for the future is generally consistent with our model of the species ecological core range with the narrowed niche width.

The constructed models of the species niche and distribution allow us to conclude that in addition to the presence of a suitable substrate (horse dung) and the habitat type (steppe or steppe communities, subject to grazing), the geographical distribution depends on a set of environmental factors that are optimal for *P. punctata*. Optimal climatic conditions for *P. punctata* in Asia are typical for steppe communities and steppe shrub thickets of intermontane depressions of Lakes Basins and lowlands between mountain ranges, as well as for light coniferous forests at the lower boundary of its distribution in the mountain forest-steppe adjacent to depressions and lowlands. The latter are subjects to the most severe anthropogenic pressure.

The data on the geographic distribution of the species in relation to the relief elevation correlates with the MaxEnt model in terms of the potential species distribution based on the bioclimatic variables.

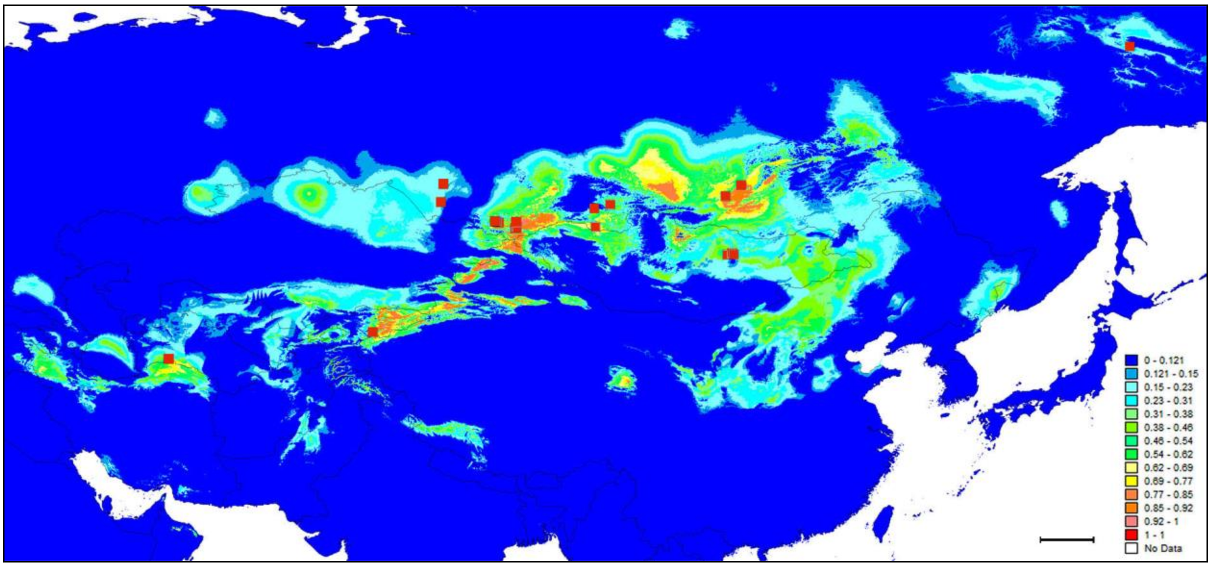

Fig. 8 – Observed presence points and the potential distribution of *P. punctata* in current climate (~1950-2000). Values in the legend are given from 0 to 1, which corresponds to the probability of presence 0-100%.

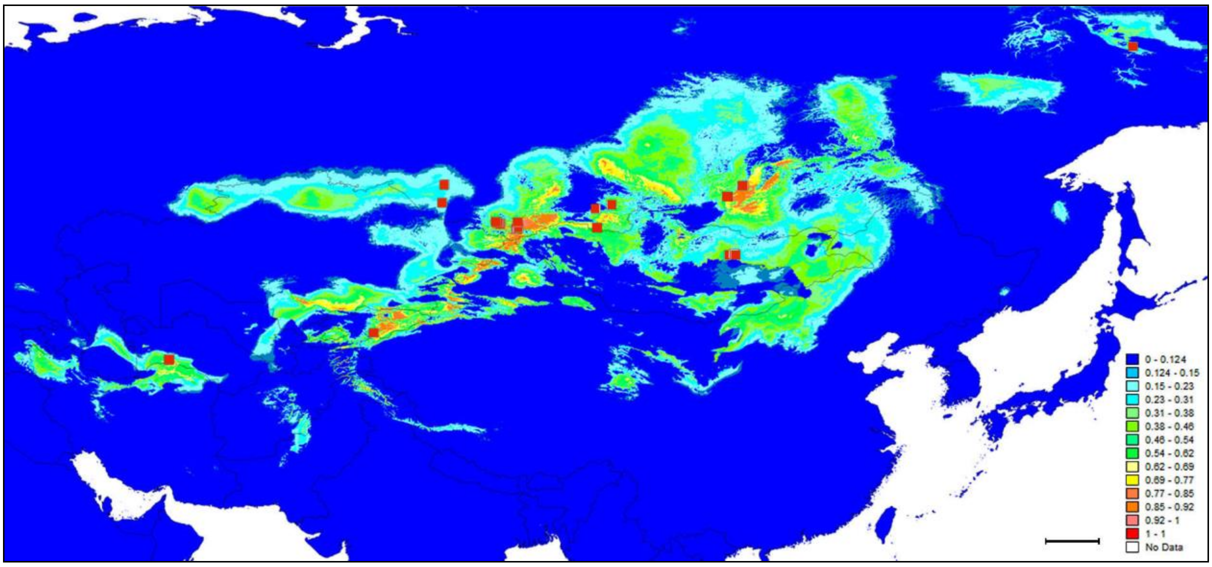

Fig. 9 – Observed presence points and the potential distribution of *P. punctata* in future climate (2100 AD). Values in the legend are given from 0 to 1, which corresponds to the probability of presence 0-100%.

Analysis of the *P. punctata* distribution within the boundaries of the Terrestrial Ecoregions of the World did not show a confinement to any particular biome. Still, most of the locations are within the boundaries of three biomes: Temperate grassland, savanna and shrubland, Montane grassland and shrubland, Deserts and xeric shrubland. A common pattern for the species is that all species habitats were associated to the vegetation type of steppe and forest-steppe. Locations within the boundaries of Temperate Coniferous and Boreal Forest occurred in the habitats affected by anthropogenic activity and grazing, subjected to steppe formation. Also, the locations were associated to river valleys and lakes, which also brings them closer to the habitats of depressions and lowlands.

Punctaporonins and other bioactive compounds of *P*. *punctata* are able to inhibit growth of potential competitor species (Anderson et al. 1984, Edwards et al. 1989, Gloer et al. 1988, Poyser 1986). The use of these compounds may be of interest for pharmaceutical industry (Granito & Lunghini 2006). In this regard, *P*. *punctata* requires conservation in natural communities, as in the future it may become a promising biotechnological object.

IUCN recommend the following conservation actions for *P*. *punctata* protection: support horse breeding under natural conditions, support the related agricultural activities, support the semi-natural habitats where *P*. *punctata* occurs, and protect the associated plant and insect species. These recommendations can be fully applied for the conservation of *P*. *punctata* in Asia.

Acknowledgements

The work was funded by RFBR and MCESSM according to the research project 19-54-44002 Mong_T.

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