

"Testing the ecological and genetic predictions of the abundant centre hypothesis: a case study of a Eurasian steppe plant"

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“Every species can live, or at least prosper, only in certain localities that bear specific conditions. ... This local distribution, or topography of plants, could form a scientific branch that is without doubts less important than botanical geography.”

(De Candolle 1855, translated from French)

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“A better understanding of spatial-temporal population dynamics across species ranges is urgently needed to address timely questions about population genetics, habitat conservation, and species responses to climate change.”

(Sagarin & Gaines 2006)

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Summary

In the face of rising human pressure on the environment, we are challenged more than ever to understand the structure and processes within species' ranges. The abundant centre model predicts that a species is most common in the centre of its distribution range, where environmental conditions for the species are at their optimum. As those conditions change over geographic space, they become eventually less favorable; leading to lower individual performance, small population sizes, and strong isolation among populations. The abundant centre model has important consequences for ecological and evolutionary processes within a species' range. In the range core, genetic differentiation among populations is expected to be low and genetic diversity within populations high. At the range edge, small population size and spatial isolation are thought to lead to genetic drift, inbreeding and impaired gene flow. As a result, peripheral populations would be characterized by high genetic differentiation and low genetic diversity. In addition, the spatial isolation and differing environmental regimes at the range edge are believed to cause a stronger adaptation in peripheral populations to their local environment.

This thesis tested predictions of the abundant centre hypothesis in European needle grass, *Stipa capillata* (Poaceae), a dry grassland plant native to Eurasia. Study populations were located in the centre of its distribution range, in Kazakhstan, Asia, where they are large and abundant, and at the range periphery in Central Europe, where they are rare and spatially isolated. The thesis presents the results of three separate but complimentary projects that tested five hypotheses.

(1) The first project tested the assumption that environmental conditions change and that performance declines at the range edge. Contrary to expectations, the results showed that out of eleven studied environmental variables, only macroclimate and soil pH differed significantly at the edge. This result might be explained by the habitat constancy rule that suggests that a species adjusts to some environmental conditions in order to keep other, important habitat conditions constant. No performance parameters except local density showed significant differences between the two regions. It appears that *S. capillata* is able to tolerate the change in macroclimate and soil pH at the range periphery by plasticity or adaptation.

(2) The second project tested whether peripheral populations differ in their genetic diversity and differentiation from central populations. Genetic differentiation was indeed higher at the range periphery, probably due to the more pronounced spatial isolation. Genetic diversity within populations was generally low in the study species but was not lower at the range edge, despite smaller population sizes and a stronger spatial isolation. This finding might suggest that population sizes at the range periphery are in fact large enough to buffer against loss of genetic diversity, or that the longevity of the study species hampers genetic loss at the range edge.

(3) In the third project, the thesis explored whether local adaptation to soil biota was more evident in peripheral than in central populations. Soil biota was chosen because it can have significant effects on plant's performance. In a greenhouse experiment over nine months, seedlings from 10 different edge and core populations were grown in their home soil and in soil from other populations, respectively. Biomass production and growth rate responded negatively to soil biota. However, local adaptation was absent in peripheral and central populations, both at the scale of ca. 10 – 80 km and of 3300 km. This result may be due to a similar soil biota composition among populations, redundancy and diffuse interactions among soil organisms, or a sufficiently high gene flow that counteracts selection regimes in plant populations.

In conclusion, this thesis has shown that the emergent hypotheses from an abundant centre model should be replaced by more nuanced concepts. In particular, future research needs to focus on the variability and interactions among environmental factors across a species' range. Furthermore, it is important to consider habitat availability in addition to physiological effects as a factor causing range limits. Life history traits deserve increased attention when predicting intraspecific genetic variation within different regions. This dissertation has shown that plant populations are not necessarily adapted to their soil biota. However, as this topic has been little explored in the past, this thesis can be an example for future research. Last but not least, discussions on the conservation value of peripheral populations should embrace the importance of non-biological values.

Zusammenfassung

Angesichts des zunehmenden anthropogenen Einflusses auf die Umwelt sind wir mehr denn je herausgefordert, die Struktur und die Prozesse innerhalb von Artarealen zu verstehen. Das „abundant centre“ Model sagt voraus, dass eine Art am häufigsten in ihrem Arealzentrum zu finden sei, wo Umweltbedingungen für sie am günstigsten sind. Mit zunehmender räumlicher Distanz würden sich diese Bedingungen ändern und für die Art immer ungünstiger werden, was dazu führt, dass Individuen eine schlechtere Kondition aufweisen, und dass die Populationen kleiner und voneinander stark isoliert werden. Das „abundant centre“ Model hat wichtige Konsequenzen für die ökologischen und evolutionären Prozesse innerhalb eines Artareals. Im Arealzentrum erwarten wir eine geringe genetische Differenzierung zwischen den Populationen und eine hohe genetische Diversität innerhalb der Populationen. Man geht davon aus, dass die kleinen Populationsgrößen und die räumliche Isolierung am Arealrand zu genetischer Drift, Inzucht und beeinträchtigten Genfluss führen. Folglich sollten Randpopulationen durch eine hohe genetische Differenzierung und eine geringe Diversität gekennzeichnet sein. Ferner sollten die räumliche Isolierung und ein unterschiedlicher Umwelteinfluss eine ausgeprägte Adaptation an die lokalen Umweltbedingungen bedingen.

Die vorliegende Arbeit testet die Vorhersage der „abundant centre“ Hypothese am Beispiel des Pfriemengrases, *Stipa capillata* (Poaceae), einer Trockenrasen- und Steppenart, die in Eurasien heimisch vorkommt. Die untersuchten Populationen befanden sich im Zentrum des Areals, in Kasachstan, Asien, wo sie groß und häufig waren, und am Arealrand in Mitteleuropa, wo sie selten und räumlich isoliert waren. Diese Dissertation stellt die Ergebnisse von drei getrennten aber aufeinander aufbauenden Projekten vor, die fünf Hypothesen getestet haben.

(1) Das erste Projekt testete die Annahme, dass sich die Umweltbedingungen am Arealrand ändern, und dass sich die Kondition der Art verschlechtert. Entgegen den Erwartungen haben die Ergebnisse gezeigt, dass von elf untersuchten Umweltparametern, sich die Randpopulationen nur durch das Makroklima und den Boden pH unterschieden haben. Dieses Ergebnis kann durch das Gesetz der Habitatskonstanz erklärt werden, welches vorhersagt, dass eine Art sich an ändernde Umweltbedingungen anpassen kann, um andere

Umweltbedingungen konstant zu halten. Nur die lokale Dichte der Horste zeigte von allen erhobenen Konditionsparametern einen Unterschied zwischen den beiden Regionen. Es scheint, dass *S. capillata* die Änderung des Makroklimas und Boden pHs durch Plastizität oder Adaptation tolerieren kann.

(2) Das zweite Projekt testete, ob sich Randpopulationen in ihrer genetischen Diversität und Differenzierung von den Zentrumspopulationen unterscheiden. Die genetische Differenzierung war in der Tat höher am Arealrand, was auf die stärkere räumliche Isolierung zurückzuführen sein könnte. Die genetische Diversität in den Populationen war insgesamt gering, aber sie war nicht geringer am Arealrand, obwohl die Populationen dort kleiner und stärker räumlich isoliert waren. Diese Tatsache könnte darauf hinweisen, dass die Populationsgrößen am Arealrand noch groß genug sind, um einen Verlust der genetischen Diversität abzumildern, oder dass die Langlebigkeit der Art solch einen Verlust gebremst hat.

(3) Im dritten Projekt untersuchte die Dissertation, ob die lokale Adaptation an Bodenorganismen am Arealrand stärker als im Arealzentrum ist. Die Bodenbiota wurde als Faktor ausgewählt, weil sie das Pflanzenwachstum entscheidend beeinflussen kann. In einem neunmonatigen Gewächshausversuch wurden Keimlinge von 10 verschiedenen Rand- und Zentrumspopulationen aufgezogen, jeweils in ihrem lokalen Boden und im Boden von anderen Populationen. Die Bodenbiota hatte einen negativen Einfluss auf die Biomassenproduktion und die Wachstumsrate. Jedoch gab es keine Hinweise, dass Rand- und Zentrumspopulationen an sie angepasst waren, weder im Maßstab von ca. 10 – 80 km, noch 3300 km. Dieses Ergebnis könnte durch eine ähnliche Bodenbiota erklärt werden, oder durch eine Redundanz und durch diffuse Interaktionen zwischen den Bodenorganismen. Ferner könnte ein ausreichend hoher Genfluss jeglicher Selektion in den Populationen zuwider gewirkt haben.

Diese Dissertation hat gezeigt, dass die Hypothesen, die sich vom „abundant centre“ Model ableiten, mit weit nuancierteren Auffassungen abgelöst werden sollten. Die zukünftige Forschung sollte sich vor allem auf die Variabilität und die Interaktionen der Umweltvariablen innerhalb von Artarealen fokussieren. Ferner ist wichtig, dass man außer den physiologischen Effekten Habitatverfügbarkeit als einen Auslöser für Arealgrenzen berücksichtigt. Bei der Vorhersage von intraspezifischer genetischer Variation in verschiedenen Regionen, sollte man Lebensmerkmalen stärker Beachtung schenken. Diese Dissertation hat gezeigt, dass Pflanzenpopulationen nicht unbedingt an ihre Bodenbiota angepasst sind. Weil jedoch diese Thematik recht wenig in der Vergangenheit erforscht

wurde, könnte diese Dissertation als ein Beispiel für zukünftige Forschung dienen. Zum Abschluss sollte erwähnt werden, dass die Diskussion um den Naturschutzwert von Randpopulationen die Bedeutung von nicht-biologischen Werten anerkennen sollte.

На фоне все возрастающего антропогенного влияния на окружающую среду, мы призваны более чем когда-либо понимать структуру видов и процессы, происходящие внутри их ареалов. Модель центрального обилия (*abundant centre model*) подразумевает, что виды наиболее обильно представлены в центре своего ареала, где условия окружающей среды для них оптимальны. Поскольку эти условия меняются в соответствии с географическим положением, они становятся менее благоприятными вдали от центра ареала данного вида. Это ведет к более низкой индивидуальной приспособленности, и, как следствие, к маленьким и сильно изолированным популяциям. Модель центрального обилия предусматривает происходящие внутри ареалов экологические и эволюционные процессы. В центре ареала генетическая дифференциация среди популяций предполагается низкой, а генетическое разнообразие внутри популяций высоким. На окраине ареала, маленькие размеры популяций и фрагментированность, очевидно, ведут к дрейфу генов, близкородственному скрещиванию и неполноценному потоку генов. В результате, периферические популяции должны характеризоваться высокой генетической дифференциацией и низким генетическим разнообразием. К тому же, пространственная изоляция и отличающиеся условия окружающей среды на окраинах ареала, вероятно, обуславливают более сильную адаптацию к локальным условиям среды.

В данной диссертации проверены гипотезы центрального обилия на примере Тырсы (European needle grass, *Stipa capillata*, Poaceae) – степного растения с естественным распространением в Евразии. Популяции этого вида исследовались в центре его ареала, в Казахстане (Азии), где они крупные и с высокой плотностью; и на краю ареала, в центральной Европе, где вид редок, а его популяции пространственно изолированы. В работе представлены результаты трех отдельных, но связанных между собой проектов, в которых проверено пять гипотез.

(1) В первом проекте проверено предположение, что на границе ареала условия окружающей среды изменяются, а приспособленность вида уменьшается. Вопреки ожиданиям, результаты показали, что из одиннадцати изученных характеристик окружающей среды, только макроклимат и кислотность почвы (pH) значительно

отличаются на границах ареала. Этот результат может быть объяснен правилом постоянства местообитаний (the habitat constancy rule), предполагающим, что виды приспосабливаются только к некоторым условиям окружающей среды для того, чтобы другие важные условия местообитаний оставались постоянными. Кроме локальной плотности популяций, ни один из параметров приспособленности не показал значительных отличий между двумя изученными регионами. Оказывается вид *S. capillata* способен выносить изменения макроклимата и кислотности почвы на периферии ареала посредством фенотипической изменчивости или адаптации.

(2) Во втором проекте проверено, действительно ли периферические популяции отличаются по их генетическому разнообразию и дифференциации от центральных популяций. Генетическая дифференциация была действительно выше на периферии ареала, вероятно вследствие более ярко выраженной пространственной изоляции. Генетическое разнообразие внутри популяций изучаемого вида было низким в целом, в обоих регионах. Интересно, что внутрипопуляционное генетическое разнообразие не было ниже на границе ареала, вопреки тому, что там популяции маленькие и более изолированные. Это открытие, очевидно, значит, что периферические популяции всё же обладают достаточно большими размерами для того чтобы препятствовать потере генетического разнообразия, или же этому способствует долгий жизненный цикл изучаемого вида.

(3) В третьем проекте диссертации было показано, действительно ли локальная адаптация к почвенной биоте более выражена на периферии ареала, чем у популяций центра ареала. Почвенная биота, как показатель, была выбрана, поскольку она может значительно влиять на продуктивность растений. В течение девятимесячного эксперимента растения из 10 разных популяций, как периферических, так и центральных, выращивались в теплице. Растения культивировались на своей природной почве и на почве из других популяций соответственно. Продукция биомассы и скорость роста находились в отрицательной зависимости с содержанием почвенной биоты. Несмотря на это, локальная адаптация отсутствовала в периферических и центральных популяциях, в обоих случаях в масштабах около 10 – 80 км и 3300 км. Этот результат можно объяснить рядом факторов, таких как, вероятно, похожим составом почвенной биоты среди популяций, большой избыточности микроорганизмов в почве, разнообразными взаимодействиями между ними, или тем,

что между популяциями растений происходит достаточно высокий поток генов, который противодействует режимам отбора.

В заключение, данная диссертация показала, что предположения модели центрального обилия и гипотезы, основанные на ней, должны быть замещены более детально исследованными концепциями. Будущие исследования должны уделить особое внимание изменчивости и взаимодействию факторов окружающей среды внутри ареалов. Более того, при изучении факторов, обуславливающих границы ареалов, важно учитывать не только физиологические эффекты, но и само наличие местообитаний. При прогнозировании внутривидовой генетической вариабельности различных регионов необходимо ставить акценты на особенности жизненного цикла растения. В диссертации показано, что популяции растений не обязательно адаптированы к их почвенной биоте. Поскольку эта тема была мало освещена в прошлом, данная диссертация может быть примером для будущих исследований. В итоге стоит подчеркнуть, что при обсуждении важности сохранения периферических популяций нужно обращать внимание также на их небиологическое значение (для эстетики, экотуризма и т.п.)

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1 General introduction

1.1 The abundant centre model

Understanding the distribution and abundance of species is one of the most essential goals in ecology (Lévêque 2003, Begon et al. 2006). Never before has this task been as important as today, in the face of global environmental change (Gaston 2003, Holt & Keitt 2005, Gaston 2009). Ecologists are challenged to make predictions on how globalization, land-use change and global warming will affect the distribution and abundance of species. Some urgent questions concern, for example, the spread of pests, diseases, and invasive species (Mooney & Hobbs 2000, Rogers and Randolph 2000), and the abundance and distribution of economically important (Iverson & Prasad 1998) and endangered taxa (Wilcove et al. 1998). In order to make accurate predictions, however, we need to understand the ecological and evolutionary processes within species' ranges (Gaston 2003).

Ecologists agree that a species' abundance within its geographic distribution range varies spatially (Hengeveld & Haeck 1982, Brown et al. 1995, Gaston 2003). It is less well known whether this variation follows a predictable pattern. A widely-believed concept is that a species' abundance is highest in the geographic core of its distribution range and declining towards the geographic periphery, where its individuals finally disappear (Wulff 1950, Tolmachev 1962, Hengeveld & Haeck 1982, Brown 1984, Lawton 1993, García-Ramos & Kirkpatrick 1997, Sagarin et al. 2006). As with many other theories in ecology, this concept is built on observations of early ecologists and biogeographers. For example, Carl Ludwig von Willdenow (1792) already noted in the eighteenth century, that some trees and shrubs of Eurasia become more rarely towards their geographic distribution limits. Similar perceptions can be found throughout the scientific literature of the nineteenth and early twentieth century (Grisebach 1847, Diels 1908, Shelford 1911, Grinnell 1922).

This simplified pattern is known today as the abundant centre model (ACM, or abundant centre hypothesis, Sagarin & Gaines 2002, Sagarin et al. 2006, Eckert et al. 2008). It is most frequently explained with reference to ecological conditions. Generally, environmental conditions are thought to vary throughout a species' range but to be at their optimum in the distribution core. With increasing distance from the core, habitat conditions change gradually

and eventually become so stressful for a species that population size and abundance decline (Shelford 1911, Tomachev 1962, Brown 1984, Brussard 1984). Such abiotic and biotic constraints at the range edge are thought to directly impair individuals at different life stages and lead to lower performance (Stott 1981, Brown 1984, Hoffmann and Blows 1994, Lesica & Allendorf 1995, Gaston 2009). So far, the abundant centre model has proved to accurately describe the abundance structure in a variety of different taxa, including carabid beetles, plants and birds in north-western Europe (Hengeveld & Haeck 1982), birds (Brown et al. 1995), and *Drosophila* flies (Brussard 1984) in North America. However, numerous counter-examples show that it should not be regarded as a general principle among organisms (Sagarin & Gaines 2002, Fuller et al. 2009).

The abundant centre model has been used as a base line for establishing hypotheses on ecological and evolutionary processes across a species' range (García-Ramos & Kirkpatrick 1997, Sagarin & Gaines 2002, Gaston 2003). However, its assumptions have rarely been tested empirically. Specifically, few studies have investigated what environmental conditions differ between the range core and edge and whether such a change would lead to a decline in performance in peripheral populations (Geber 2008). Most studies inspecting environmental conditions across a species' range have focused on macroclimatic properties; an approach with a long tradition in ecology (Salisbury 1926, Woodward 1987, Sykes et al. 1996, Gaston 2003). In contrast, empirical studies on topographic and edaphic habitat conditions are still scarce (but see recent advances by Hájková et al. 2008, Leuschner et al. 2009, Eckhart et al. 2010). Although some studies have assessed a species' performance across its range their results have so far been mixed, as reviewed by Sexton et al. (2009). Thus, we lack a clear understanding of the variability of both environmental conditions and performance in central and edge populations.

1.2 Genetic diversity and structure in peripheral vs. central populations

The protection of genetic diversity has high priority for conservation (Bowman 1996, Frankham et al. 2009). Genetic diversity has been shown to positively influence individual fitness and reproduction (Leimu et al. 2006, Crawford & Whitney 2010, Kotowska et al. 2010), and is considered as a prerequisite for evolutionary change (Blows & Hoffmann 2005). The ultimate strategy for the conservation of genetic diversity depends on its partitioning among hierarchical levels. High among population genetic diversity calls for the protection of

all respective populations, whereas high within population diversity requires only some populations to be protected (Gibbs 2008).

The variation in genetic diversity and genetic differentiation across species' ranges is not well understood. Theoretically, small populations should be subject to enhanced genetic drift and inbreeding, which in turn lower genetic diversity and increase genetic differentiation (Ellstrand & Elam 1993). Under the isolation by distance model, pronounced spatial isolation should also cause high genetic differentiation among populations. If we apply these basic genetic principles to the abundant centre model, we would expect genetic diversity to be lower and genetic differentiation to be higher at the range edge than in the core (Hoffmann & Blows 1994, Eckert et al. 2008).

Although peripheral populations of many species have been found to show the expected decline in genetic diversity and increase in genetic differentiation (e.g. Lammi et al. 1999, Jump et al. 2003, Eckstein et al. 2006, Michalski & Durka 2007), there is increasing doubt to what extent this correlation is a general rule. In a review by Eckert et al. (2008), 36% of considered studies did not find the expected decline in genetic diversity at the range edge, and 30% failed to detect higher genetic differentiation. Notwithstanding the ambiguities, the assumption that peripheral populations are genetically more depauperate and differentiated than central populations can be frequently found across the conservation literature (Safriel et al. 1994, Fraser 2000, Channell 2004). In fact, high genetic differentiation at the range edge has been used as a justification for the conservation of peripheral populations (Lesica & Allendorf 1995). Resolving patterns of genetic diversity and structure across distribution ranges would thus not only benefit our basic understanding of evolutionary processes but would also have important implications for conservation.

1.3 Local adaptation at the range edge

Local adaptation is the process and result in which resident genotypes are favored by selection in their local habitat conditions over non-local genotypes (Kawecki & Ebert 2004). Locally adapted populations are considered to have a high potential for evolutionary divergence (Channell 2004) and are thus regarded as important units for conservation (Crandall et al. 2000, McKay et al. 2001). Local adaptation has important consequences for restoration practice, as well. It requires that for a successful transplantation, reintroduced material is derived primarily from nearby sites (Hufford & Mazer 2003, Bischoff et al. 2010).

A common perception is that local adaptation is particularly high at the range periphery (Levin 1970, Lesica & Allendorf 1995, Channell 2004). This claim has been justified based on the assumptions of the abundant centre model. The higher spatial isolation among populations, low gene flow and different environmental selection regimes are thought to favor local adaptation at the range edge (Levin 1970). In addition, it has been suggested that because peripheral populations are potentially more adapted to stressful conditions than central populations, they can enable the species to respond to future environmental change (Fraser 2000, Channell 2004). Both arguments have been used to justify the conservation of peripheral populations (Lesica & Allendorf 1995).

Generally, local adaptation seems to be moderately common in plant species but constrained by population size, as shown in a meta-analysis ($n = 35$ published studies) by Leimu & Fischer (2008). However, there are few comparative studies on local adaptation specifically at the range edge and in the range centre (Geber 2008, Kawecki 2008). In a study on *Opuntia fragilis*, Loik & Nobel (1993) have shown that populations at the northern distribution periphery are locally more adapted to climate than range central populations from more southern latitudes. By contrast, Santamaría et al. (2003) failed to detect adaptation to local climatic conditions in central and peripheral populations of *Potamogeton pectinatus*, whereas Mimura & Aitken (2010) have shown that adaptation was equally present among populations of *Picea sitchensis* throughout its range.

1.4 Study objectives

The aim of this dissertation was to evaluate five hypotheses that are based on the abundant centre model. I chose populations of the European needle grass, *Stipa capillata* L. (Poaceae, grass family), as my study objects. This species was well suited for my aims as it is one of the most important species of Eurasian dry grasslands and its distribution in Europe and Asia is well known (Lavrenko 1970). In addition, *S. capillata* is red listed in many European countries (see chapter 1.6 below) and thus is of high interest for conservation. My approach was a comparative one, in which I contrasted populations in the range centre, in Kazakhstan, Asia, with those at the range periphery, in Central Europe.

The first project examined whether populations at the range edge differed in their environmental conditions from those in the range centre. Furthermore, this project tested the assumption that individual performance and local density decline in peripheral populations in

comparison to central populations. The second project inspected whether genetic differentiation was higher and genetic diversity lower in peripheral than in central populations. The third project investigated whether plants in populations at the range edge were locally more adapted to their soil biota than plants from populations in the range core. The results of this thesis will increase our understanding about ecological and evolutionary processes across a species' range.

1.5 Study species

The study species, *Stipa capillata*, was described by Linneus (von Linné 1762) from Central Europe (“in Germania, Gallia”, p. 116). It is the type species for the section *Leiostipa* (Dumortier 1823). Like all members of the *Stipa* genus, *S. capillata* is characterized by an inflorescence with single flowers in a stalked floret, and an awn attached to the lemma (Tsvelev 1976). A conspicuous character of the species is the glabrous and long (10 - 20 cm) awn (Komarov 1934, Tsvelev 1976). In its vegetative form, *S. capillata* can be distinguished from other members of the *Leiostipa* section by the fact that its lower most nodes are always enclosed in a leaf sheath and that the ventral leaf surface is not covered by hairs (Komarov 1934, Tsvelev 1976).

This perennial plant forms tussocks, in which individual shoots are tightly arranged (Tsvelev 1976). As clonal growth by spreading tillers is not known for this species, it can be assumed that each individual represents a genet. Its leaves are complanate to involute, with continuous sclerenchyma on the dorsal side (Florineth 1974). Flowers are pollinated by wind from the end of June to the beginning of August. The species is also known to be facultatively cleistogamous, meaning that its flowers can be self-pollinated in its sheath. Seeds are enclosed in the lemma, ripen at the beginning of August and September and are dispersed by wind, in animal fur and in clothes. *S. capillata* was reported to be tetraploid ($2n = 44$, Skalińska et al. 1968).

Stipa capillata is native to large areas of Asia and Europe (see also distribution maps in chapters 2-4). Its native westernmost occurrences are found in Spain (Tutin et al. 1980). Its eastern distribution reaches Yakutia, in Russia (Tolmachev 1974). The northernmost populations are located in the Upper Yenisei region, in the Krasnoyarskiy Kray, Siberia, Russia (Malysheva & Peshkova 1990). The southernmost distribution extends to Pakistan (Cope 1982) and Nepal (Press et al. 2000).

The study species grows in nutrient-poor dry grasslands of the temperate climate zone. This habitat is characterized by high insolation, strong daily temperature amplitudes, and low water availability, especially in summer (Medwecka-Kornaś & Kornaś 1966, Hensen 1995, Ellenberg 1996). *Stipa capillata* can grow on a variety of different substrates. In Asia, it has been reported from tchernoziem and sandy to loamy castanoziem soils (Walter 1974, Dieterich 2000, Perezhagin 2007, Schwahn 2007). In Central Europe, it can occur on carbonate rich marls and rendzina soils over limestone (Krausch 1955, Medwecka-Kornaś & Kornaś 1966, Becker 1999), carbonate rich sand deposits (Walter 1974, Mucina & Kolbek 1993), and gypsum outcrops (Medwecka-Kornaś & Kornaś 1966).

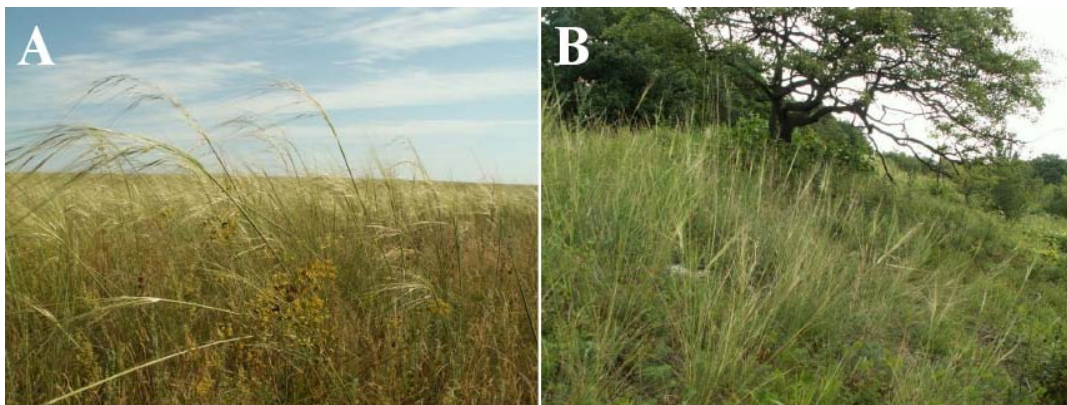


Fig. 1.1. *Stipa capillata* growing in the steppe of the Naurzum region, Kazakhstan (July 2007), and in a preserved dry grassland fragment around Freyburg, eastern Germany (July 2010).

Eurasian dry grasslands have been classified by different approaches in the past (Gibson 2009). In the framework of the phytosociological vegetation classification, *S. capillata* is known from different orders of the *Festuco-Brometea* Br.-Bl. & Tx. class. Near the northwestern edge of its range in Europe, it occurs foremost in the continental dry grasslands, *Festucetalia valesiacae* Klika, and the continental sand grasslands *Festucetalia vaginatae* Soó (Mahn 1965, Mucina & Kolbek 1993, Ellenberg 1996, Chytrý et al. 2007). In Asia, dry grasslands have not been thoroughly classified using the phytosociological approach but it can be assumed that *S. capillata* is a typical species of the continental steppes, the *Helictotricho-Stipetalia* Toman (Mirkin & Naumova 1998). In the framework of the dominant vegetation

classification approach of Karamysheva & Rachkovskaya (1973), this species forms different communities of its own steppe formation.

In the moist climate of Central Europe, forests are the dominant natural vegetation (Ellenberg 1996). Natural dry grasslands are rare and confined to xeric habitats, such as rock outcrops (Medwecka-Kornaś & Kornaś 1966, Ellenberg 1996). In the warm Atlantic period, shortly after the Pleistocene (ca 7500–3000 BP) natural dry grasslands were more widespread in Europe (Hensen 1995, Ellenberg 1996). As climate turned cooler and moister, dry grasslands were replaced by more mesic vegetation and retreated to naturally xeric sites, such as rock outcrops (Ellenberg 1996). However, large scale deforestation in the Medieval Ages and human land use by mowing and livestock grazing enabled dry grasslands to expand and become established as semi-natural vegetation. These anthropogenic dry grasslands became more frequent than natural dry grasslands in Central Europe but their area declined in the last century owing to the abandonment of traditional land use (Poschlod et al. 2005). Today, succession by scrub and tress and eutrophication are the main threats to dry grasslands in Central Europe (Hillebrand 2008). In the European Union, dry grasslands are an endangered habitat and under legal protection (referred to as Sub-Pannonic steppic grasslands, Natura 2000 code 6240, Annex I, Council Directive 92/43/EEC of 21 May 1992 on the Conservation of natural habitats and of wild fauna and flora).

In Kazakhstan, dry grasslands (or more commonly referred to as steppe in this region) are a natural vegetation type as the climate is too dry to support forest vegetation (Karamysheva & Rachkovskaya 1973, Walter 1974). The history of steppe in this region is less well known than in Europe. Presumably, steppes date back to the Pliocene and have experienced little transformation during the ice age (Frenzel 1968). Over many centuries, steppes have been grazed with moderate intensity by the livestock of nomadic Kazakhs. It is only during the Soviet period of the last century that large areas of steppes began to be converted into agricultural land (Dieterich 2000). Since the breakup of the Soviet Union, large scale state farming was abandoned and fields started to undergo succession (reversion) to steppe vegetation (Schwahn 2007).

The detailed abundance structure within the range of *S. capillata* has never been studied. However, we know that in its range core, in the steppes of Asia, it is one of the most common plant species (Lavrenko 1970, Walter 1974, Fig. 1.1A) and is not categorized as rare in Russia (Golovanov et al. 1988) or Kazakhstan (Bykov 1981). In contrast, at its north-western distribution edge in Central Europe, it is confined to small and scattered dry grassland patches

(Fig. 1.1B), and is red-listed in Austria (Niklfeld et al. 1999), the Czech Republic (Holub & Procházka 2000), Germany (Ludwig & Schnittler 1996), Poland (Mirek et al. 2006), and Switzerland (Moser et al. 2002). Thus, the populations at the distribution periphery in central Europe and in the distribution core in Kazakhstan offered an ideal framework to study the ecological and genetic predictions of the abundant centre hypothesis.

2 Similar performance in central and range-edge populations of a Eurasian steppe grass under different climate and soil pH regimes

- Ecography (In Press) –

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2.1 Abstract

The abundant-centre hypothesis predicts that changing environmental conditions are detrimental to a species' abundance and performance toward the periphery of its range. We tested these predictions for the perennial grass *Stipa capillata* L., a species that is commonly found in steppes of Asia but is rare at its north-western range edge, in Central Europe. We compared 21 populations in dry grassland fragments in Central Europe and 20 populations in steppe habitats of Kazakhstan. We studied 15 plant performance traits both *in situ* and under laboratory and common greenhouse conditions, including local density, plant size and biomass production, seed size, weight and viability. To assess environmental conditions, we assembled data on topography, soil properties and climatic parameters. Using variance components analysis and multivariate methods we analyzed whether plant performance and environmental attributes differed more, as predicted, between the core and peripheral regions or whether they differed more among their subregions or populations. Additionally, we tested whether performance was affected by the same set of environmental predictors in each region. As expected, macroclimatic conditions showed a significant difference between the two regions (annual mean temperature, annual precipitation). The only other measured environmental variable that differed significantly between the two regions was soil pH, which

was lower in core-range populations. Contrary to our expectations, plant performance traits were virtually unchanged between the range periphery and centre. Our findings thus do not support the notion of reduced performance at the range edge. Instead, our data lend support to earlier theories of relative habitat constancy, suggesting that peripheral populations can shift to other habitats through plasticity or adaptation.

Keywords: Abundant centre hypothesis, distribution edge, geographic distribution range, macroclimate, niche, soil pH, *Stipa*.

3 Increased genetic differentiation but no reduced genetic diversity in peripheral vs. central populations of a steppe grass

- American Journal of Botany (Minor revision) -

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3.1 Abstract

Intraspecific genetic diversity is essential for the performance and evolution of species. Populations at a species' range periphery receive considerable attention in biogeography and conservation because they are smaller and spatially more isolated than central populations, a pattern expected to lead to higher genetic differentiation and lower within population genetic diversity. We tested these predictions in central and peripheral populations of the Eurasian steppe grass *Stipa capillata*. We analyzed AFLP fingerprint patterns in 319 individuals from 20 large and abundant populations in the core, in Kazakhstan, and 23 small and isolated populations at the periphery, in Central Europe. We employed a band-based approach to obtain genetic diversity estimates and to assess genetic differentiation among populations by examining F_{ST} values, a neighbor-net network and an AMOVA. As expected, genetic differentiation among populations was significantly larger at the range periphery ($F_{ST} = 0.415$) than in the range core ($F_{ST} = 0.164$). In contrast to predictions, however, we found similarly low genetic diversity within central (proportion of polymorphic bands = 21.9%) and peripheral (20%) populations. Higher genetic differentiation in the small and spatially isolated peripheral populations is likely driven by genetic drift and reduced gene flow due to a complex landscape structure and the abandonment of traditional management regimes. With regard to unchanged genetic diversity, it appears that life history traits like longevity or still sufficiently large population sizes could allow *S. capillata* to escape deleterious effects at the range edge.

Keywords: Abundant center hypothesis, AFLP, dry grassland, fragmentation, genetic differentiation, genetic diversity, Poaceae, range periphery, steppe, *Stipa*.

4 Prevailing negative soil biota effect and no evidence for local adaptation in a widespread Eurasian grass

- PLoS ONE (Minor revision) -

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4.1 Abstract

Soil biota effects are increasingly accepted as an important driver of the abundance and distribution of plants. While biogeographical studies on alien invasive plant species have indicated coevolution with soil biota in their native distribution range, it is unknown whether adaptation to soil biota varies among populations within the native distribution range. The question of local adaptation between plants and their soil biota has important implications for conservation of biodiversity and may justify the use of seed material from local provenances in restoration campaigns. We studied soil biota effects in ten populations of the steppe grass *Stipa capillata* from two distinct regions, Europe and Asia. We tested for local adaptation at two different scales, both within (ca. 10–80 km) and between (ca. 3300 km) regions, using a reciprocal inoculation experiment in the greenhouse for nine months. Generally, negative soil biota effects were consistent. However, we did not find evidence for local adaptation: both within and between regions, growth of plants in their ‘home soil’ was not significantly larger relative to that in soil from other, more distant, populations. Our study suggests that negative soil biota effects can prevail in different parts of a plant species’ range. Absence of local adaptation points to the possibility of similar rhizosphere biota composition across populations and regions, sufficient gene flow to prevent coevolution, selection in favor of plasticity, or functional redundancy among different soil biota. From the point of view of plant - soil biota interactions, our findings indicate that the current practice of using seeds exclusively from local provenances in ecosystem restoration campaigns may not be justified.

Keywords: Dry grassland, geographic distribution range, plant-soil feedback, range edge, soil organisms, soil sterilization, *Stipa*.

5.1 General discussion

This dissertation used populations of a Eurasian steppe plant as study objects to test five ecological and genetic hypotheses for the core and edge of a species' distribution range (Table 5.1). Only one hypothesis was fully verified (higher genetic differentiation at the range edge). The perceptions that environmental variables generally change and that performance declines at the range periphery was only partially substantiated. The study rejected the hypotheses that genetic diversity is lower and local adaptation higher in peripheral populations (Table 5.1). Thus, this dissertation has shown that the abundant centre model and the hypotheses that are built on it must be treated with caution (Sagarin & Gaines 2002).

Table 5.1. Overview of the hypotheses and results of this dissertation.

Hypothesis	Hypothesis verified?
- Environmental conditions in peripheral populations differ from those in the centre.	Partially (only macroclimate and soil pH)
- Performance is lower in peripheral than in central populations.	Partially (only local density)
- Genetic diversity is lower in peripheral than in central populations.	No
- Genetic differentiation is higher among peripheral populations than among central populations.	Yes
- Local adaptation is higher in peripheral populations than in central populations.	No

A fundamental assumption of the abundant centre model is that environmental conditions change from the geographic distribution centre to the periphery. Although this notion can be frequently found across the scientific literature, our knowledge on this subject is still insufficient and mainly limited by the lack of large scale environmental data. In the last decades, digitized data has become available on species occurrences (e.g. Global Biodiversity

Information Facility, www.gbif.org, accessed on January, 20 2011; Edwards et al. 2000), macroclimate (e.g. Hijmans et al. 2005), and GIS-based topography. However, information on other environmental variables, such as on microclimate and soil edaphic properties, is missing, remains unavailable in digitized form for most regions, or is only available at a coarse scale for well-studied countries (e.g. for Germany: Kühn 2007). One solution to this problem is the use of indicator values, expert based estimations of a species' response to environmental gradients, such as developed by Ramensky et al. (1956) for Russia, Ellenberg (1974) for Central Europe, Landolt (1977) for Switzerland, and Hodgson et al. (1995) for Great Britain. Prinzing et al. (2002) have used this approach to examine the behaviour of species' ecological niches in different regions. However, these indices are available only for some (mostly European) countries, and have furthermore been criticized as being circular and as having been rarely substantiated with measurements (Rydin & Jeglum 2006). Thus, in order to accurately describe the environmental variation within species ranges, we still rely on field studies.

Studying only parts of a species' range always bears the risk that results represent only sampling artifacts. One might argue, for instance, that *S. capillata* occurs indeed on higher soil pH in steppes of Kazakhstan but that the relevant study populations were not included in the sampling scheme. However, the studies by Karamysheva & Rachkovskaya (1973) on steppe vegetation in Central Kazakhstan indicate that *S. capillata* does not grow on carbonate rich soils in this region. In order to thoroughly investigate environmental variability across the range of *S. capillata* it is necessary to compare its niche optimum and breadth along the entire gradient (see Hájková et al. 2008). This method would require extensive sampling, including on sites where the species is not present. In Europe, large vegetation data bases (see <http://www.iavs.org/ResourcesDatabases.aspx>, accessed on January, 20 2011) would facilitate such comparisons, at least for some variables that are commonly measured, but such data bases have yet to be compiled for Asia.

If one seeks to find direct mechanisms causing range limits, documenting environmental shifts at the range limit will not be sufficient. First of all, this approach runs the risk that the respective environmental variable simply correlates with the unknown causal factor (Parmesan et al. 2005). In addition, this dissertation has shown that a change in macroclimate and soil pH at the range periphery does not necessarily translate into direct effects on a species' performance; most studied performance traits in peripheral populations of *S. capillata* did not differ from those in central populations – a finding that contradicts the expectations of the abundant centre hypothesis. Certainly, it is possible that differences are

manifested in other, unstudied traits, such as in more variable birth and mortality rates, or more variable seed bank dynamics (Gaston 2009, Kluth & Bruehlheide 2005). However, a review by Sexton et al. (2009) suggests that only 60% of all considered studies ($n = 26$) have found population dynamics to be more variable at the range edge.

Contrary to the abundant centre hypothesis, Holt & Keitt (2000) have proposed that range limits can evolve without any ecophysiological stress. Such a scenario would occur if local conditions in patches are still favorable but habitat patches scarce. In the case of *S. capillata*, two reasons speak in favor of habitat limitation as a more important factor than ecophysiological stress in determining its north-western distribution limit. First, this dissertation has indicated that environmental conditions are generally favorable within Central European dry grassland patches. Second, the surrounding matrix of unsuitable habitats, such as forests and agricultural fields, precludes theoretically any expansion. As most dry grasslands in Central Europe are semi-natural, habitat availability ultimately also depends on human intervention.

The deleterious effects of small population size and high spatial isolation on genetic diversity are well-known problems in population genetics and conservation (Ellstrand & Elam 1993). This danger has been pointed out for dry grassland plants in Europe by Picó & van Groenendael (2007). Using AFLP fingerprint data in 40 populations of *S. capillata*, this study confirmed the prediction of higher genetic differentiation among peripheral populations but it contradicted the expectations of lower genetic diversity at the range edge. In fact, peripheral populations had the same genetic diversity as the larger and spatially better connected central populations. These findings show that small population sizes and spatial isolation alone are insufficient predictors of within-population genetic diversity. Instead, they stress the importance of other factors in shaping genetic diversity across the range. In the case of *S. capillata*, it is likely that contemporary or past population sizes at the range periphery are/were large enough, and/or that the longevity of the species counteracts any loss of genetic diversity.

This study explored genetic diversity and differentiation at the northwestern distribution range of *S. capillata*. One should be careful not to apply these findings to range limits of other regions, as these might be characterized by different population structures, topography and landscape. For example, the southern range limit of *S. capillata* in deserts of Central Asia is characterized by an open landscape matrix, which should potentially facilitate gene flow and

lower genetic differentiation. Studies covering all range limits are laborious but will provide a more accurate understanding of genetic processes across a species' range.

Populations at the periphery of a species' distribution range receive extensive attention in conservation due to their potential significance for divergent evolution (Levin 1970, Lesica & Allendorf 1995). Their pronounced spatial isolation is believed to lead to a stronger adaptation to local environmental conditions than in central populations. However, this study found no evidence that peripheral populations of *S. capillata* were locally more adapted to their soil biota than central populations, despite a stronger spatial isolation at the range edge. Thus, spatial isolation alone is an insufficient predictor for local adaptation.

On the one hand, the absence of local adaptation in *S. capillata* can be accredited to the soil biota. A homogeneous soil biota composition, redundancy and diffuse interactions among soil organisms could account for a lack of adaptation. Our knowledge on the geographical variation in soil biota effects will benefit from an identification of all members of a soil community. In the past, such identifications were restricted only to those organisms that could be cultured (Osborn & Smith 2005). The development of high throughput molecular tools, such as microarrays (Andersen et al. 2010) will provide valuable insights in that respect, in the future. On the other hand, the lack of local adaptation can potentially also be attributed to the plant populations. Theoretical models in evolutionary biology have shown that local adaptation at the range edge can be prevented by gene flow among populations (García-Ramos & Kirkpatrick 1997, Kirkpatrick & Barton 1997, Bridle & Vines 2007, Kawecki 2008). The fingerprint analysis of *S. capillata* showed that its populations at the north-western distribution edge are genetically more isolated. However, direct measures of gene flow through paternity or maternity analysis would provide a more accurate assessment of gene flow (Lowe et al. 2004, Hamilton 2009). However, one should bear in mind that gene flow is not the only key to our understanding of local adaptation. Local adaptation can establish even if gene flow is high provided that selection is strong enough (Mimura & Aitken 2010).

5.2 Implications for conservation

In most parts of the world, threatened species receive legal protection under international and domestic laws that prohibit their exploitation, trade and destruction (van Heijnsbergen 1997). Unlike globally rare species, peripherally rare species can be scarce only within the political boundaries they occur in and be much more common outside the border. The conservation of such peripherally rare species has been the subject of intense debates (Hunter & Hutchinson

1994, Lesica & Allendorf 1995, Fraser 2000). On the one hand, the practice of conserving peripherally rare species has been accused of being parochial (meaning disproportionately local in its aims; Hunter & Hutchinson 1994, Wells et al. 2010). The most frequent argument against conservation of peripheral populations leveled by opponents is the waste of resources at the expense of globally rare species (Hunter & Hutchinson 1994, Dudley 1995, Rodrigues & Gaston 2002, Channell 2004). On the other hand, proponents have argued that geographically peripheral populations are important from an evolutionary perspective. Assuming an abundant centre model, they have claimed that the high genetic differentiation and different selection regimes at the range edge make peripheral populations important units for the persistence and evolution of a species, especially in the face of future global warming (Lesica & Allendorf 1995, Fraser 2000, Hampe & Petit 2005, Kawecki 2008).

At first glance, the high genetic differentiation among peripheral populations of *S. capillata* may seem to speak in favor of their conservation. However, it is unclear to what extent neutral genetic differentiation translates into meaningful effects for future speciation processes. There was no indication that *S. capillata* populations at their range periphery in Central Europe suffer from the genetic consequences of small population size and spatial isolation. As the species is likely limited by habitat availability, habitat loss might pose a more important risk for this species in Central Europe. The lack of stronger local adaptation to soil biota at the range periphery should not be equated with the general absence of stronger evolutionary dynamics at the range periphery. It is possible that peripheral populations are locally adapted to other environmental factors, for example to local climate (Macel et al. 2007), or leaf pathogens and seed predators (Alexander et al. 2007, Laine 2007).

When discussing the biological value of peripherally rare species one needs to bear in mind that these taxa can have important services for other organisms, including those at other trophic levels. For example, it is possible that *S. capillata* serves as a mutualist for the establishment of other plants species (Callaway 2007), and that its leaves and caryopses offer nourishment for birds and mammals. Insect pollinated dry grassland plants have also an important role for pollinators (Goverde et al. 2002, Steffan-Dewenter & Tschardtke 2002). Peripherally rare species can also make up a large portion of all rare species in a country. For example, in Germany, peripherally rare species make up 70% (832 species) of all rare plant species (Welk 2001). If peripherally rare species were no longer to be accorded conservation status, this would endanger a large portion of Germany's biodiversity. Furthermore, the protection of single species is tightly connected with the protection of its habitat. Consequently, conserving peripherally rare species means also maintaining habitat diversity.

Biological arguments have dominated the discussion on the conservation of peripherally rare species but non-biological arguments can be equally meaningful. In this respect, one can think of several additional arguments in favor of the conservation of peripheral populations. First, peripherally rare species can be beneficial for humans (or have “instrumental” values, see van Heijnsbergen 1997, Alexander 2008). Using the example of dry grassland plants in Central Europe, these rare species can have aesthetic value for local human populations and spur ecotourism in the region. This is probably best exemplified by the showy plant *Adonis vernalis* which year by year during its flowering time draws admirers to the “*Adonis*” trails in north-eastern Germany. Another important argument is the intrinsic value of peripherally rare species. Loosely speaking, conserving peripherally rare species based on their intrinsic value means to conserve them for their own sake and acknowledging their right to persist (Elliot 1997). Last but not least, conserving peripheral populations can be valuable because nature conservation has a high moral esteem among humans (Elliot 1997). The variety of these reasons should not be overlooked in the discussion on the conservation of peripherally rare species.

In conclusion, this dissertation has shown that the hypotheses based on the abundant centre model are in parts too general and too simplistic to accurately predict ecological and genetic patterns across a species’ range. Detecting simple rules in nature is a holy grail in science, but nature, it seems, is more complex than we sometimes like to think.

6 Literature

Note: The transliteration of Russian titles into English follows the BGN/PCGN romanization system.

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Erklärung

Hiermit erkläre ich, dass die vorliegende Arbeit von mir bisher weder der Naturwissenschaftlichen Fakultät I – Biowissenschaften der Martin-Luther-Universität Halle-Wittenberg noch einer anderen wissenschaftlichen Einrichtung zum Zweck der Promotion vorgelegt wurde.

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Halle, den 28.01.2011