Trait evolution and genetic structure of a native plant species in diverse urban environments

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論　文　内　容　の　要　旨

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論文題目（外国語の場合は，その和訳を併記すること。）
Trait evolution and genetic structure of a native plant species in diverse urban environments
（多様な都市環境における在来植物の形質進化と遺伝構造）

論文要旨(1198/2000字)

The global expansion of urban areas has led to habitat loss, fragmentation and environmental change, contributing to a decline in biodiversity. Urban development affects both biotic and abiotic factors, resulting in increased temperatures, known as the urban heat island effect, increased CO2 concentrations, and higher levels of soil and water eutrophication. The invasion of plants into urban areas has exacerbated the threat to native species, leading to a decline in plant species richness, particularly in regions with expanding impervious developed areas. Thus, there is an urgent need to understand how organisms adapt to human-dominated ecosystems, making it a central concern in ecology and evolutionary biology.

Evolutionary ecologists have extensively documented examples of organisms adapting to urban environments, but comprehensive studies of adaptive evolution driven by urbanisation remain limited, and there are several challenges to understanding urban evolutionary biology. First, many studies use dichotomous or distance gradient comparisons, making it difficult to distinguish whether trait evolution is a response to urbanisation-induced habitat change or to specific habitat conditions. Comparisons between urban and non-urban populations within the same habitat type are recommended to clarify this distinction. Second, recent research reveals significant trait differences not only between urban and rural populations, but also between different urban habitat types. The increasing diversity of developed land within cities promotes habitat diversity, potentially leading to trait diversification across different urban

habitat types, an aspect that requires further investigation. Third, although previous research has shed light on the variation in adaptive responses to urban environments among different functional traits, there is still a gap in our knowledge of whether evolution occurs independently within individual traits or cooperatively across multiple traits. Therefore, gaining insight into intraspecific variation in multiple traits along urban-rural gradients is crucial for understanding the mechanism of urban adaptation. The common garden experiment is a widely used method for assessing whether genetic factors contribute to trait divergence between urban and rural plant populations. However, challenges exist in determining the relationship between relative fitness and observed traits, and conducting only common garden experiments may not distinguish robust trait divergence from phenotypic plasticity. Therefore, the comparison between quantitative trait divergence (Q_{ST}) and genetic divergence (F_{ST}) using neutral genetic markers, which provides insight into whether traits are adapting to local environments or evolving neutrally. Comparing genetic diversity and structure between urban and rural populations also provides crucial insights into plant adaptations to urban environments and neutral evolution. Urban development is also one of the factors that influence reduced gene flow and increased genetic drift within populations. Comparing genetic structures between urban and rural populations, and between different urban habitat types, helps to understand whether the observed trait divergence occur due to a single origin or to parallel processes.

In this thesis, I describe the effects of urban development and the creation of habitat diversification on the evolution and/or plastic responses of multiple functional traits and population genetic traits in the annual native species *Commelina communis* along an urban-rural gradient within the Kyoto-Osaka-Kobe metropolitan area.

In Chapter 2, I conducted both a field survey and a common garden experiment to test the effect of increasing developed land area on several vegetative traits of plants living in the semi-natural grassland surrounding the agricultural land along an urban-rural gradient. The combination between the field survey and the common garden experiment showed that fewer leaf production in urban populations is likely to evolutionary response, and larger plant height and leaf area were plastic response for urban environments. In addition, the trait correlative relationships along an urban-rural gradient suggested that the probability of trait correlation evolution in urban population. Thus, my results showed that environmental changes associated with urbanisation can exert pressure on native annual plant species.

In Chapter 3, I investigated the effects of urban habitat diversification on the vegetative, phenological and reproductive traits of an annual native species through the implementation of a common garden experiment. I also conducted a comparison of Q_{ST} and F_{ST} to determine whether the traits measured were the result of local adaptation or neutral evolution. Urban habitats were characterised by higher soil pH, and urban parks and roadsides were shaded and/or dry, in contrast to rural habitats. Urban populations, especially those near roadsides, exhibited traits such as increased plant height, reduced number of shoots and leaves, and larger leaves compared to their rural counterparts. In addition, populations in urban agricultural areas exhibited a delayed flowering phenology compared to other urban population types. Notably, urban park populations often exhibited intermediate characteristics between those of rural populations and other urban types. The relationships between plant height, leaf/shoot number and flowering phenology were suggested to be key factors in explaining trait divergence in urban habitats. The Q_{ST}-F_{ST} comparisons, coupled with the relationships between traits and environmental factors, strongly suggested that local adaptation to eutrophic and/or shaded urban environments is likely to have driven the observed trait divergence in different urban populations.

In Chapter 4, I investigated whether urban habitat diversification and variation in landscape configuration between populations affected genetic diversity and structure using multiplexed inter-simple sequence repeat genotyping. No significant differences in genetic diversity and structure were observed between different habitat types. Isolation by distance not only between same habitat types, but also among different habitat types was also not observed. However, variation in landscape configuration, especially forest and developed land areas, appeared to promote genetic divergence. The study species has a mixed mating system and my results exhibits a high inbreeding coefficient, suggesting that *C. communis* may mitigate the negative effects of the urban environment through its high selfing rate.

Overall, my results suggest that environmental and landscape changes associated with the creation of diverse urban habitat types acted as selective pressure for multiple functional traits in the annual native plant species (Chapter 2, 3) and there were specific trait syndromes for each urban habitat types (Chapter 3). Notably, increased soil pH and the creation of artificial shaded environments effected on plant size, leaf/shoot production and reproductive phenology. In addition, intraspecific trait variation in both the field and the common garden experiment and genetic divergence were observed along an urban-rural gradient (Chapter 2, 4), indicating the potential involvement of overall environmental change in plant trait evolution and landscape heterogeneity, particularly variation in forest and developed land cover, was found to influence genetic structure.

My findings of no significant differences in genetic diversity and structure between different habitat types (Chapter 4), despite trait divergence leading to local adaptation (Chapter 3), and the plastic response of *C. communis* vegetative traits to the urban environment in the field (Chapter 2) provide new insights. Polyploidy traits emerge as key elements for urban adaptation compared to diploid species, given the versatility of polyploid species in different environments, their wider distribution, lower susceptibility to urbanisation-related effects on genetic diversity, and higher tolerance to environmental stress. Considering the probable tetraploid nature of *C. communis*, known for its higher environmental stress tolerance and wider ecological range than diploid plants, and the distinct distribution of *C. communis f. ciliata*, closely related with fewer chromosomes, predominantly in rural environments along urban-rural gradients, the importance of ploidy in urban adaptation is highlighted. Future studies should examine different ploidy levels and manipulate environmental factors to gain deeper insights.

（注）3,000～6,000字（英語の場合は1,000～2,000語）でまとめること。

［課程博士用］

論文審査の結果の要旨

氏　　名	中田 泰地		
論文題目	Trait evolution and genetic structure of a native plant species in diverse urban environments (多様な都市環境における在来植物の形質進化と遺伝構造)		
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要　　旨

本博士論文では、在来1年生植物ツユクサにみられる都市環境への適応進化の実態を明らかにしている。20世紀以降、都市への人口集中(都市化)が世界的に進行し、現在、世界人口の約60%が都市に暮らしている。都市域では、人間活動の利便性向上のため、自然・半自然生態系の人工地への転換が進み、植物の生育地は減少・断片化する一方、公園など新規に造成される生育地もみられる。都市生育地では、土壌の中性化や乾燥など生育地環境の改変も起きている。そのため、都市では多くの在来植物種が減少・局所絶滅する一方で、都市環境への適応をみせる植物種も存在することが、近年報告されている。本論文では、京阪神地域の都市から里山にかけて生育するツユクサを対象種として、都市－里山間の形質分化や異なる都市生育地間の形質分化が、適応進化によるものなのかについて、野外調査、温室栽培実験および集団遺伝学解析を組み合わせて検証している。本論文は5章構成で、序論である第1章、都市農地・公園・路傍の集団でみられる形質変異が遺伝変異か否か、局所適応の産物といえるか否かを検証した第2-3章、都市域と里山域の集団遺伝構造や遺伝的多様性を比較した第4章、以上の個別研究で得た結果の総括を行う第5章、謝辞、引用文献及び付録資料から構成されている。

まず、1章では、植物における都市適応に関する先行研究を総括し、既往研究では、特定の形質のみに着目したものが多いこと、都市部および周辺の農村部に生育する集団の2項比較から都市適応の研究がなされたものが多いことを明らかにし、複数形質を同時に対象とした研究が少なく、都市でみられる残存農地、公園、路傍など異なる環境をもつ多様な生育地への多様な都市適応という視点でなされた研究が十分されていないことを指摘している。2章では、都市から里山にかけて、

農地に生育するツユクサ集団を対象に、複数の栄養成長形質を測定し、都市農地における生育地周辺の人工地増加の形質変異への影響を調べている。その結果、植物高と葉面積に関しては、周辺の人工地増加による可塑的な増加がみられた。一方、都市農地集団では、遺伝的変異として葉数や比葉面積の減少がみられることを明らかにしている。3章では、都市農地に加えて、都市の公園・路傍の集団も対象に、野外での環境要因測定と温室内での複数形質の測定を行い、都市生育地間では土壌pH・水分含量および光環境が有意に異なること、ツユクサの植物高や葉数・地上茎数、開花開始日などの形質に生育地間に差が見られることを発見した。詳細には、里山集団に比べて、全ての都市生育地集団において、植物高が高い、地上茎数や葉数が少ない、葉サイズが大きいなどの共通した傾向がみられることを発見している。さらに、都市農地では他の集団に比べて開花が遅い、路傍ではより顕著な上方成長がみられるなどの特徴があり、公園集団は、里山と他の都市集団の中間的な形質がみられることを明らかにしている。また、遺伝的形質分化(Qst)と中立的な遺伝分化(Fst)の比較により、以上の形質における生育地間変異は、各生育地への局所適応であることを示唆する結果を得ている。4章では、MIG-seq法を用いた集団遺伝学解析の結果から、ツユクサの里山－都市集団間で遺伝的な多様性に差はなく、際立った遺伝分化も見られないことを示し、都市化は京阪神地区のツユクサ集団の遺伝的特徴に大きな影響を与えてないことを明らかにした。また、生育地周辺の人工地の増加や森林の減少は集団間の遺伝分化を促進しうることも明らかにしている。5章は、以上の研究結果を受けて、阪神地区の都市部に生育するツユクサにみられた適応的な形質変異や遺伝的多様性、遺伝構造と本種の持つ自殖性や異質倍数性との関係についても詳しく議論し、本研究の発見の一般性や発展性について述べている。

本博士論文は、以上の通り都市における植物の適応進化についての既存の知見を補完し、これまで、ほとんど研究がなかった多様な都市生育地への適応について、表現型形質の野外・温室における測定と集団遺伝解析を組み合わせて研究を行うことで、都市環境は在来植物の可塑的な形質応答や遺伝的な形質適応を促進することを示唆した。またこの際、異なる都市生育地への適応放散ともいえる形質分化が見られることを明らかにした点は新規性がみられる。これにより、人間により創出された都市環境が、植物の多様な応答や進化をもたらしうるという視点を与えたという点を鑑みて、人間環境学の観点においても高く評価できる。

なお、本論文を構成する各章(第2-4章)の研究内容の出版状況は、2章はWoS誌のPlant Biology誌に掲載され、4章についてはWoS誌のEcology and Evolution誌に掲載されている。3章は投稿論文を準備中である。以上、本論文の研究結果が国際的に見ても高いオリジナリティを有することが、研究の出版状況を鑑みていえる。

Taichi N & Ushimaru A (2024) Trait variation along an urban–rural gradient in Asian dayflower: the contribution of phenotypic plasticity and genetic divergence. **Plant Biology** 26:74–81. (査読付き)

Taichi N, Nakahama N, Ohmido N & Ushimaru1 A (2024) Habitat diversification associated with urban development has little effect on genetic structure in the annual native plant *Commelina communis* in an East Asian megacity. **Ecology and Evolution** 14:e10975. (査読付き)

以上より、学位申請者の中田泰地は、博士(理学)の学位を得る資格があると認める。

レフェリー付きの論文の発表について，記載すること。