Temporal analysis of plant community changes documenting climate and urban practice impacts in cities. The case of Paris (France) over a 136-year period

Machon Nathalie, Gallant-Canguilhem Matthieu, Ropars Lise, Jeanne Vallet

ORIGINAL ARTICLE

Temporal analysis of plant community changes documenting climate and urban practice impacts in cities. The case of Paris (France) over a 136-year period.

Running title: Comparison Parisian plant communities 1884-2021

Machon Nathalie[1*], Gallant-Canguilhem Matthieu[1], Ropars Lise[1], Vallet Jeanne[2]

[1] *Centre d'Ecologie et des Sciences de la Conservation, Muséum national d'Histoire naturelle, Sorbonne Université, Centre National de la Recherche Scientifique, 57 rue Cuvier, 75005 Paris, France*

[2] *Conservatoire Botanique National du Bassin Parisien, Muséum national d'Histoire naturelle, 57 rue Cuvier, 75005 Paris, France*

*For correspondence: E-mail nathalie.machon@mnhn.fr

- **Background and Aims:** Besides its intrinsic value, urban biodiversity participates to city dwellers' better health and quality of life. One method to define which factors are driving biodiversity is to determine the changes in communities between two time-periods and confront them with the environmental and/or practice changes that have occurred at the same time.
- **Methods:** We compared the changes that occurred in the Paris (France) plant communities at a 136-years interval, thanks to two inventories performed in exactly the same streets, wharves and squares, according to exactly the same protocol. We examined which species disappeared, endured and appeared from the 19th century onwards, determined the traits of these different groups of species and deduced which factors could have driven the shifts in the composition of the Parisian weed communities.
- **Key Results:** The total number of species (about 190 species) remained relatively similar over a 136-year timespan. Nevertheless, a turnover of about 50% of the species happened. The differences between the 1884 and 2021 floristic data mostly followed climatic and human activity changes i.e. the current flora seems to be better adapted to a warmer climate and shifts in soil qualities. The differences in weeding practices also modeled the new plant communities.
- **Conclusions:** This study is documenting changes in plant communities over such a long period. Generally, comparable lists of urban data are scarce because former naturalists rarely studied city areas and seldom detailed reproducible protocols. In our case, the protocol was strictly reproducible and accurate enough to enable a comparison. The results inform on the impact of global and local changes on biodiversity. It also provides important clues about how to better integrate biodiversity in urban projects for the ecosystem to function better and to improve future city dwellers' well-being.

Key words: Functional traits, streets, docks, squares, Joseph Vallot, Ellenberg indicators, Jaccard's distances.

Introduction

Urbanization is one of the principal reason for land use changes worldwide to bring about biodiversity alterations (Maxwell *et al.,* 2016). However, biodiversity is present in cities. Besides its intrinsic value, it also participates to city dwellers' better health and quality of life (Aerts, Honnay and Van Nieuwenhuyse, 2018). Territorial collectivities have to preserve it in order to participate to the general conservation of biodiversity and to give citizens the best possible life-conditions. For these reasons, it is necessary to determine what the main drivers of the composition of natural urban communities are, and particularly the composition of plant communities, which are key elements for biodiversity. Their state shapes the quality of all networks and food chains interactions. In cities, they are composed of both cultivated and spontaneous species, and among them, native and exotic ones. Cultivated species are species planted by humans for food or ornamental purposes. Spontaneous ones are those that grow naturally, originated locally or that landed by themselves from outside the city, or even spilled over from gardens.

As conceptualized by (Aronson *et al.,* 2016), spontaneous urban vegetation is the result of processes by which species filter which bare human disturbances and city environment. Most plant species in cities dwell in diverse habitats (Lundholm and Marlin 2006) including parks, public gardens (Shwartz *et al.,* 2013), flowerbeds, lawns, river banks, railways and green spaces at business sites (Serret *et al.,* 2014). Among these habitats, public spaces such as streets, squares and riverbanks offer a multitude of micro-green spaces that can harbor a number of plant species, especially when management and trampling are limited (Pellegrini and Baudry 2014);(Schmidt, Poppendieck, and Jensen 2014). In streets of cities like Paris –

except for alignment trees, which are planted mainly to decorate and provide shade in summer – plants are rather wild and grow spontaneously in every crack in pavements, walls and roads. Up till now, few studies have described the species that grow in such public spaces and have determined the drivers of their communities' compositions (Omar et al. 2018) (Lundholm and Marlin 2006).

One method to define which factors are driving biodiversity is to determine the changes in communities between two time periods and confront them with the environmental and/or practice changes having occurred at the same time, and examine how adjustments may have taken place (Grimm et al. 2008). Thus, comparing urban plant communities, observed at more than a one-century interval, make up extremely informative case studies of the effects of local and global changes on biodiversity (Salinitro et al. 2019a).

Trait-based approaches can even more accurately provide general rules for community ecology (Cadotte, Carscadden, and Mirotchnick 2011), as well as a more mechanistic understanding of community assembly and disassembly – particularly in the context of global climate change (Mcgill *et al.*, 2006), (Williams *et al.*, 2019). Thus, in our study, reproductive and ecological traits have been investigated to explain interspecific variations at temporal scale, in response to environmental and anthropogenic changes as well.

Among ecological traits, Ellenberg's indicator values (EIV) (Ellenberg 1991) describe in which environmental conditions plant species grow in Central Europe (Diekmann 2003). They can be used as a numerical system to classify species' habitat niches (Silvertown et al. 2006) i.e., what their peak of occurrence are in terms of light availability (L), temperature (T), atmospheric (Ma) and soil moisture (Ms), soil reaction (R), soil fertility (N) and salinity (S). Furthermore, dependence of plant species on pollinators is also a trait that can characterize their ecological needs. For each of these traits, their means per community can be calculated. Comparison in time or space can characterize changes among communities.

This paper presents the changes that occurred in the Paris plant communities at a 136-year interval, thanks to the existence of an inventory published in 1884 in a book entitled "Essay on the flora of the Paris pavement limited to outer boulevards, or Catalog of plants that grow spontaneously in streets and on wharves" (Vallot 1884), by a well-known French botanist Joseph Vallot. In 2021, we followed in his footsteps, using the same inventory protocol at exactly the same places. We used the trait-based approach to understand how environmental changes may have affected biodiversity from that time onwards.

(Salinitro et al. 2019b) have listed different studies published on the same subject in other European cities. None of them held such precise data, performed exactly the same protocol in exactly the same places and used species' characteristics to inform the recorded changes and thus characterize global changes' impacts on communities. Our study is more precise than previous ones in that it was based on data related to the abundance of species by their presence in a large sample of streets, wharves and squares in Paris, and not just in general, as was the case, for example, in Italy in Bologna (Salinitro et al. 2019b), Brussels in Belgium (Godefroid 2001), Plzen in the Czeck Republic (Chocholoušková and Pyšek 2003) or Zurich in Switzerland (Landolt E 2000).

[Figure 1]

Comparing both available datasets, the present paper reports the changes that happened over 136 years in the plant communities found in 52 public spaces, all found in Paris, France: streets, squares and Seine river's wharves. The study only focused on the spontaneous flora and excluded cultivated/ornamental vegetation. The habitats sampled all belonged to the micro-structures that support vegetation, i.e., cracks in asphalt, the base of alignment trees, the feet of walls, the spaces between paving stones… We examined which species were growing in the Parisian public spaces in the late 19th century, which ones disappeared, endured, and emerged from that time on. We determined the traits of these different groups of species and deduced which factors could have driven the shifts in Parisian weed communities' compositions.

MATERIALS AND METHODS

Study site

The study is located in the capital city of France (the World Geodetic System 1984 reference is 48° 50′ 26.91″ N, 2° 23′ 17.46″ E), within the limits Paris used to have just before the annexation of the bordering cities, which took place in 1860 (map fig 1, list Annex 1). The area covered an area of approximately 3.5 km², in the city's densest districts.

During the 19th century, on emperor Napoleon III's command, the Paris center was deeply modified by Baron Haussmann (Haussmann 1890). He opened wide avenues, created many grounds and green spaces, built pavements for pedestrians, planted trees along the main streets and erected the famous Paris Haussmann buildings. He resurfaced the streets, wharves and squares by re-paving and asphalting the main roads. By 1884, the work was completed.

In 1884, the human density was approximately 80,000 habitants/km². It was lower in 2021, when there were around 20,500 inhabitants/km² (according to INSEE i.e. the French National Institute for Statistics and Economic Studies, 2017, http://www.insee.fr).

In 2021, the heritage of Baron Haussmann is still significant. Urbanization has not changed much in 136 years. Districts have more or less the same shape today as they used to at the end of the 19th century. All the streets that existed in late 19th century still exist, except one (rue Bunant).

Floristic data

1884's inventories

In 1884, Joseph Vallot published the list of the plants growing in 52 public spaces (PS): 35 streets, 15 riverbanks and 2 squares in Paris (France), comprised in the study site. He collected the data in all the habitats in streets, squares and river wharves: 1° in the cracks between cobblestones in streets and quays, on banks; 2° stones on quays; 3° plants on small walls; 4° the rare bare soils; 5° the soil around tree bases along boulevards and avenues.

Among the plants inventoried, we removed all trees and shrubs because we considered they had probably been planted. We also removed the only mention of a non-angiosperm plant (i.e., *Equisetum arvense*). We have updated each species' names according to the French list TAXREF 15.0 (https://inpn.mnhn.fr/telechargement/referentielEspece/taxref/15.0/menu). Only one species namely *Carex muricata* L., observed by Vallot, remains questionable as it is a historical name covering several taxa (*Carex otrubae, divulsa, leersii, pairae, spicata*…).

Joseph Vallot did not mention when he carried out his inventories. As he did not record any spring or autumn species, we assumed that he collected his data over one growing season between May and August, over a single year, around 1884.

2021's inventories

We researched the names and locations of each public space (PS) (street, wharf and square) visited by Vallot. Some of them had changed name since then, but only one street had to be discarded (Rue Bunant), as it no longer existed in 2021. We thus carried out our inventories in all streets but one of them within the same limits as Vallot's.

We listed all the herbaceous angiosperm species between May and August 2021, except ornamental species. When necessary, we used the app Pl@ntNet® to ensure the validity of our identifications.

A matrix of the presence/absence of each species, in each of the sampled locations, at each period: in Annex 1, it is presented with species in the rows; and in the columns, the streets/wharves/squares as found in 1884 or 2021.

Regarding the native status, we used the database from the National Botanical Conservatory of Parisian Basin CBNBP (http://cbnbp.mnhn.fr/cbnbp/), which indicates whether each species is considered as native or exotic in France.

Ellenberg indicator values and species dependency on pollinators

For each species, seven Ellenberg indicator values were collected using the R package TR8 (Bocci 2015): temperature, light, nutrient, soil reaction and humidity, atmospheric humidity, and salinity indicator values from the French database Baseflor (Julve Philippe 1998), and also their dependence on pollinators for their reproduction (SPD). Ellenberg's temperature indicator values are species-specific indices describing preferences along climatic gradients (Ellenberg 1991). They characterize the optimum temperature class for a species' growth and survival, among 9 classes ranging from "alpine to nival, altimediterranean floor" (T-number = 1) to "thermomediterranean to subarid floor" (T-number = 9). The soil reaction gradient ranges from 'high acidity, never moderately acidic or alkaline' (R- number= 1) to 'alkaline and calcareous conditions, only calcareous soils' (R- number = 9). The soil moisture covers species growing on dry soils (Ms- number = 1) to species growing on wet, hypoxic soils (Ms- number = 9). EIVs for nitrogen/nutrients span species growing on poor soils (N- number 1) to species growing on nutrient- rich soils (N- number = 9). Light species growing in deep shadow have an EIV of (L- number = 1), while species growing in full light have an EIV of (L- number = 9). For all these indicators, we calculated the community-mean preferences per street in 1884 and in 2021 (hereafter CMP) i.e., the mean of EIV of all species inventoried in each street (Garnier *et al.,* 2004).

We also classified species on the basis of their dependence level to pollinators for their reproduction. Following the methods of (Duchenne, Martin, and Porcher 2021), plants were scored as more or less pollinator dependent. Pollen vectors (i.e., insects, wind or self-fertilization) were retrieved from the Baseflor (Julve Philippe 1998) Ecoflora (http://ecoflora.org.uk/ Fitter and Peat 1994) and BiolFlor (www.biolflor.de Klotz, Kühn, and Durka 2002; Kühn, Durka, and Klotz 2004) trait-bases. To integrate the sometimes-contradictory data indicated by the different databases, the authors calculated a single variable as the percentage of times "insects" proved to be a pollen vector for a given species, across all databases. Their "species pollinator dependence" (SPD) was 100% when they were reportedly completely pollinator dependent, i.e., allogamous and self-incompatible. It was 0% when they were reported as only reproduced by selfing and/or pollinated by the wind. For each street, wharf and square, we also calculated the mean dependence to pollinators and compared them between the two periods.

All the data were treated using R packages *rstatix* (https://rpkgs.datanovia.com/rstatix/) and (http://haozhu233.github.io/kableExtra/). The tests performed on mean Ellenberg indicator values and mean dependence to pollinators by public space were Wilcoxon's paired series median comparison tests, since both normality and homoscedasticity hypotheses were not validated for the 1884 data set.

Floristic distances among streets and among wharves between the two periods

To properly characterize inventories in relation to each other, we calculated pairwise Jaccard's distances between the 1884 and 2021 street floras, using the R *vegan* package (https://github.com/vegandevs/vegan). With those distances, we drew the two dendrograms using the R *dendextend* package (https://cran.r-project.org/package=dendextend) with Ward's method, which minimizes the intraclass inertia and maximizes the interclass inertia in order to obtain the most homogeneous closures and subgroups possible.

RESULTS

General floristic trends

[Figure 2]

A total of 282 species had been listed in Paris over both inventories (Fig 2). One third (95 sp.) were only found by Vallot in 1884 and not in the 2021 inventory. Among them, according to the French databases (MNHN & OFB (Ed) 2003), eighteen of them disappeared from Paris during the 20th century. One third (94 sp.) were only found in 2021 and had not been seen by Vallot. Among them, 46 appeared in Paris during the 20th (39 sp.) or 21st centuries (7 sp.). And one third (93 sp.) were found in both inventories. The Dice coefficient (Dice 1945) i.e. their similarity was thus 0.496.

In the 1884 pool of species, 10.70 % were exotic (i.e., arrived in France after 1492). In 2021, this rate was 23.53%.

The mean number of species growing in these streets and the wharves increased a lot, from 5.23 sp and 30.52 sp respectively in 1884 to 32.05; and 40,47 sp in 2021. In both squares, species richness remained relatively identical, with a mean of 31 and 31.5 species.

Mean trait analyses

[Table 1]

[Figure 3]

Analyses of comparisons of mean Ellenberg indicator values of plants in the Parisian public spaces detected significant differences between street, wharf and square communities between the two periods (Fig 3). In particular, they revealed a significant increase in temperature preference between the one in the 19st century to the other in 21st (the mean EIV passing rising from 5.21 to 5.69, p-value < 0.001). In the same way, analyses revealed that 21st century plants preferred drier (EIV passing from 4.75 to 4.73, p-value=0.013) and more alkaline soils (mean EIV passing from 5.82 to 6.24, $p < 0.001$). Dependence on pollinators also seemed to have increased between these periods (the mean dependence increasing from 36.39% to 45.17%). Preferences for light, salinity, atmospheric humidity and nitrate did not seem to have changed significantly between these two periods (tab 1 and figure 3).

Floristic distances

[Figure 4]

[Figure 5]

Except for one street inventoried in 2021, we found a clear differentiation of floristic composition between these two periods in streets and Seine wharves (Figures 4 and 5). Each street and wharf were floristically more similar to the other streets and wharves of its period than to itself at a 136-year interval. The distribution of species is completely changed between the two periods. The streets that were floristically similar are not the same currently. The average floristic distance is greater in streets in 1884 than in those in 2021, probably due to the low number of species per street found in the 19th century.

Discussion

The inventory performed by Vallot in 1884 followed an intense urbanization process that occurred over the 19th century and completely changed the shape of the city. Our inventories occurred in a very similar territory, from an urbanistic point of view. Thus, differences between the 1884 and 2021 floristic data mostly followed climatic and human activity changes. Contrary to other studies on other cities conducted worldwide, the present results pointed out that the total number of species (about 190 species) remained relatively similar over a 136-year timespan. Nevertheless, there was a turnover of about 50% of species, only half of them identical, and the other half exclusive to one of the two period inventories. However, even if some of those exclusive species already existed or still exist in Paris, they were only found in one of the two inventories. To explain such a turnover, it should be noted that beyond their mere presence, species abundance, and thus detectability, may have changed with time. Usually, variations of species abundances are due to stochastic processes or are linked to environmental changes or practices. In any case, a study of the databases containing all the data from inventories carried out in Paris over time from the 17th century onwards, suggested this: 18 species became extinct in Paris; 39 (species) emerged during the 20th century and 7 in the 21st century. In particular, the number of alien species doubled (representing from 10.70% to 23.53% of total species).

This 50% turnover is lower than turnovers found in Bologna and in Plzenˇ in Czech Republic (Salinitro et al. 2019b) and (Chocholoušková and Pyšek 2003) where similarity indices were only 35% and 43% in 120 years and in 60 years exceeded the ones in Brussels (a 79.48% similarity) (Godefroid 2001).

In contrast to these previous studies in other cities, we directly compared the plant community indices in public spaces between the two time periods. This provides more accurate information than simply comparing species' average preferences in the overall lists. Actually, we incorporated variations in species abundance at the city level and highlighted more subtle processes than just the appearance or disappearance of species.

Floristic distances among streets and wharves during both periods revealed high communities' differentiation over more than one century (fig 3 and 4). The flora in each space resembles that in other spaces of its time, much more than does its own flora at 136-year intervals.

The most obvious sign of the current flora's adaptation to a warmer climate is the increase in mean EIV values concerning plant communities' temperatures (Fig 2). Some species, because they were well-suited to cold climates, disappeared from Paris (e.g., *Carum carvi* or *Turritis glabra*) or displayed reduced abundance. For example, *Centaurea jacea* and *Fallopia convolvulus* decreased their occurrences by 2.5 between 1884 and 2021 (3,9 □to 1.6)□.

Conversely, species well-suited to hot climates arrived recently from warmer regions in the world (e.g., *Senecio inaequidens*, from South Africa) or their abundance increased (e.g., *Hordeum murinum* multiplied its occurrences by 2.5 between these two periods).

Changes in city planning also impacted street plant communities. For example, communities' better tolerance to drier soils is observed, though annual rainfall amounts increased very slightly over one century, from 605 to 615 mm/year on average, between 1884 and 2021, according to MétéoFrance (i.e. the French organism for climate survey https://meteofrance.com/) data. However, maximum rainfall also increased (from 29.33 to 40.63 mm in 136 years, according to MétéoFrance), as did soil impermeability, with paved areas being transformed into asphalted areas. This transformation mainly followed the May 1968 demonstrations, during which students used paving stones as projectiles to attack law enforcement officers. As a result, more rainwater ran off into sewer systems and rivers, probably leaving little water available for soil and plant hydration. Wharves have also been channelized, leading to the disappearance of more or less aquatic species, like *Rorippa x anceps* and *amphibia*, or *Rumex hydrolapathum*. Recently, *Portulaca oleracea* and *Senecio inaequidens*, plants particularly adapted to dried soils, have invaded the French capital's pavements.

In the same way, the massive use of construction materials has caused the alkalization of (cement, concrete, etc...) soils. Plant communities seem to be more and more adapted to basic soils. Among the plants specializing in acid soils, *Scleranthus annuus* disappeared from Paris more than a century ago, and *Rumex acetosella* is now very rare in streets.

In contrast to what authors had found in the other cities (Godefroid 2001), (Chocholoušková and Pyšek 2003) and (Salinitro *et al.*, 2019b) we did not find any changes in communities' tolerance for light. It should be noted that buildings did not change in size and streets kept the same width from the end of 19th century onwards. Trees had also been planted before Vallot's inventories. Light has therefore probably not changed since then. However, as in other cities, no differences were found concerning communities' sensitivity to atmospheric humidity and salinity (Godefroid 2001).

Community characterization in terms of pollinator dependence revealed a significant difference between the two periods (around 40% on average). According to (Ropars et al. 2019), cities harbor diverse plant species that flourish all year long because they apply low pesticide policies and are subject to heat island effect. Hence, they provide resources for pollinators throughout the year and create favorable conditions for the maintenance of diverse pollinator communities (Harrison and Winfree 2015). We wish we could have compared these rates with other data for other cities or other environment types, but it seems they do not yet exist in the literature.

Here are the three specific human activities supposed to have modified public spaces' plant communities: means of transport; food trade; and weed control. In more than one century, horse-drawn vehicles were replaced by combustion engine automobiles. On the one hand, with the disappearance of horses from Parisian streets, their fodder and dung no longer provide abundant natural fertilizers. On the other hand, current car emissions tend to enrich the soil with nitrates. Thus, preference for soil richness does not seem to have changed over 136 years. Nevertheless, plants from horse forage seeds, such as *Avena sativa* and *Phleum pratense*, are no longer observed in Paris.

This species turnover detected in Paris over 136 years may also reflect the changes in food trade experienced as of the early 20th century. It is estimated that 95% of the fruit and vegetables consumed in the capital were produced more or less locally. Indeed, the market garden production areas constituted a green belt, justified by the size of the city's population; hence of the Parisian market; and also by the use of the city's waste as fertilizer (Moreau and Daverne 1845). The streets adjacent to these gardens probably received the seeds produced by crops there, thus extending their range to the most urbanized areas. These discharges from gardens may also have occurred during the transport of foodstuffs or seeds to points of sale such as markets or traders' carts. Thus, Vallot was, in his inventory, able to list lentils (*Lens culinaris*) or asparagus (*Asparagus officinalis*) in some of the streets – vegetables that we did not find during our inventorying.

Weeding and street cleaning are probably the practices with the greatest impact on biodiversity changes in Paris as of the 19th century. Over paved streets, sweeping machines were used when possible, otherwise they were cleaned by hand, by teams of men and women equipped with efficient brushes or birch brooms, on an everyday basis (Vallot 1884) (Haussmann 1890). Since then, pavements have gradually been covered with bitumen or tar and the local authority has continued to weed streets and pavements with more or less drastic techniques, depending on financial and human resources, as well as inhabitants' and borough councils' sensitivities. Herbicides have been increasingly implemented. On 1 January 2017, the adoption of the Labbé law, which aims to better control the use of phytosanitary products on the French territory, greatly modified public spaces maintenance. Discontinuing the use of chemical products has led Paris to manage its spaces differently. According to Parisian public spaces' managers, weeding is more seasonal and therefore much less frequent (2 or 3 times a year on average) than in the 19th century. It has become mainly mechanical, with the help of tools capable of tearing and brushing the pavement.

Thus, our results showed that Parisian pavements and wharves hosted a richer flora in the 21st century than they did in the 19th, with more species depending on pollinators. We should specify, however, that inventories were carried out during the COVID-19 pandemic crisis, when street use and management may have had a specific effect on biodiversity's quality. Nevertheless, since the abandonment of herbicides on cities' public spaces, the flora has already been found to be enriched.

Conclusion

This study is documenting changes in plant communities over such a long period. The existence of comparable lists of data are scarce because former naturalist rarely studied urban areas and seldom used or outlined reproducible protocols in detail. In our case, the protocol was strictly reproducible and sufficiently precise to allow comparison.

A welcome surprise: the present Parisian communities were richer than they seemed to be in the late 19^{th} century. It is probably due to changes in weeding intensity between these two periods. It is only recently that laws beneficial to biodiversity enacted against using pesticides in urban public territories have had an impact. As a result, the Parisian flora did not depauperate over time, which is heart-warming compared to what is observed in all ecosystems worldwide. The arrival of many exotic species offsets the loss of local ones (if they did not cause it) and enabled biodiversity to adapt to warming and other global changes experienced by our cities. Clearly, it enabled insect communities to endure and ensure pollination services.

We hope that other policy changes and a better integration of biodiversity in development projects will lead to even better biodiversity quality and better ecosystem functioning, thereby fostering future city dwellers' well-being.

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List of figures

Table 1: Wilcoxon's paired series median comparison tests: PD is the pollinator dependency; L light; T temperature; Ha atmospheric humidity; Hs soil humidity; pH soil pH; N nitrate and Sal salinity Ellenberg indicator values.

	1884	2021	u-stat	p-value
PD (%)	36.39±20.6	45.13±4.56	434.0	0.02
L	7.13±0.4	7.15±0.21	558.0	0.591
T	5.21±0.27	5.69±0.16	34.0	<0.001
Ha	4.68±0.55	4.65±0.18	756.0	0.545
Hs	4.75±0.69	4.73±0.16	929.5	0.013
pH	5.82±0.54	6.24±0.17	186.0	<0.001
N	6.73±1.26	6.76±0.24	782.0	0.4
Sal	0.23±0.27	0.16±0.08	698.5	0.743