

# Ecological Niche Differentiation Among Six Annual Lythrum Species in Mediterranean Temporary Pools

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# Abstract

The ecological niche defines the favorable range of a species in a multidimensional space of ecological factors that determine the presence and function of individuals. This fundamental concept in ecology is widely used to understand plant species coexistence and segregation. In this study we test for ecological differentiation among six annual *Lythrum* species that are characteristic of temporary pools in the South of France, where they either coexist or occur separately. We first analysed the co-occurrence of species at two different geographical scales: cluster analyses of species presence in 10 km grid cells and coexistence in 0.25m<sup>2</sup> quadrats within populations of each species. Second, for three to nine populations of each species, we quantified a range of biotic and abiotic parameters using point contacts and soil measurements in three 0.25m<sup>2</sup> quadrats per population. We performed PCA on all variables, and analysed each variable separately to compare the ecological niche features of the six species. A phenological index was assessed for the plant community of each site. We detected highly localised niche differentiation in terms of soil pH (all species) and for a range of variables among pairs of species. The six species also showed marked differences in flowering period relative to the mean and variability of flowering time in their local community. These fine-scaled niche differences are associated with phylogenetic distances among species and may contribute to species' coexistence. These results are integrated in a conservation management plan for the habitat of the rarest species in this group.

# Introduction

The concept of the ecological niche has long been a central tool in the science of ecology and evidence has steadily grown for the role of niche differentiation in species coexistence (Silvertown 2004). Formalised by Hutchinson (1957) the niche represents the multidimensional space of ecological factors in which a species can persist and function. Such discrepancy in the realized niche may enable species coexistence through resource partitioning (Silvertown 2004), influence population demography (Angert 2009), modify flowering and reproduction phenology (Bykova et al. 2012) and regeneration (Grubb 1977). Several recent studies also illustrate the pertinence of studying ecological niche differentiation among closely related species and among populations of individual species to examine evolutionary potential (Tuomisto 2006; Anacker and Strauss 2014; Grossenbacher et al. 2014; López-Alvarez et al. 2015; Papuga et al. 2018; Thompson 2020).

In plants, the wide range of ecological factors that determine the niche of individual species render niche description a complex issue (Pulliam 2000). Although they are often used to study niche variation, broad habitat units or vegetation types do not provide the correct scale to identify the precise ecological niche of plants (Hall et al. 1997; Lavergne et al. 2004; Miller and Hobbs 2007; Papuga et al. 2018; Thompson 2020). Likewise, large-scale climatic variables, although they may partially explain distribution limits, do not allow a precise clarification of niche differences (Diniz-Filho et al. 2009; Lira-Noriega and Manthey 2014) and provide only limited insights into our understanding of fine-scaled population processes (Curtis and Bradley 2016; Papuga et al. 2018). In fact, the sessile life form of plants makes it essential to identify the niche where plants grow because of the potential effect of highly localised ecological

variation on plant performance (Lönn and Prentice 2002; Jusaitis 2005). Among the different parameters involved, soil nutrient content (Paoli et al. 2006), pH (Hájková and Hájek 2004) and texture (Tuomisto 2006), hydrology (Silvertown 2004, Silvertown et al. 2015) and mineral characteristics (Lavergne et al. 2004; Papuga et al. 2018) are all well known to contribute to niche differentiation among species and populations.

Mediterranean climate regions are characterised by their sharp seasonality and most particularly the summer drought that has a major influence on plant ecology and evolution (Thompson 2020). In this context, Mediterranean temporary pools are an illustration of a wetland habitat that has a particular seasonal regime with strong consequences for plants (Bagella and Caria 2012). Following flooding in winter, they experience drying and severe drought during the summer. The vegetation of this habitat is thus subject to extreme variability in local ecological conditions, resulting in a particular flora with a predominance of annual species and a long-lived seed bank (Brock et al. 2003). There has thus been much interest in the diversity of species and their strategies in the communities of Mediterranean temporary pools (Deil 2005; Pinto-Cruz et al. 2009; Molina 2017). Although it is clear that ecological variables determine spatial and seasonal variation in the composition of plant communities in Mediterranean temporary pools (Bonis et al. 1995; Rhazi et al. 2009; Vogiatzakis et al. 2009; Caria et al. 2013; Rocarpin et al. 2015), the processes underlying the coexistence of closely related species in this ecosystem have received little attention other than a study of the genus *Lasthenia* in vernal pools of California by Emery et al. (2012).

The genus *Lythrum* has roughly 10 annual species that inhabit temporary pools and ephemeral wetlands around the West Mediterranean and Central Europe (Castroviejo Bolibar et al. 1997; Grillas et al. 2004; Morris 2007; Tison et al. 2014). These species differ markedly in their distribution and abundance; several are (extremely) rare (e.g. *L. flexuosum* and *L. thesioides*) whilst others are more common and widespread, e.g. *L. hyssoipifolia* that is considered as an invasive species outside of Europe and the Mediterranean region. An analysis of the germination niche, which is known to be important for community dynamics in temporary pools (Bliss and Zedler 1997; Valdez et al. 2019), has revealed marked differences in the strategies of four different species in terms of their temperature requirements and stratification dependence for germination (Gazaix 2019). However little is known concerning the fine-scaled ecological niche of these species during establishment and reproduction.

The objective of this paper is to quantify differences in the micro-ecological habitat of six annual *Lythrum* species in order to assess the possibility of fine-scaled ecological niche differentiation of these species in Mediterranean temporary pools. This study involved three lines of investigation. First, we analyse the spatial structure of plant coexistence to describe whether species occur together on two different scales, a biogeographic scale (co-occurrence in 10km grid squares) and a microhabitat scale (coexistence in 0.25m<sup>2</sup> quadrats). Second, we quantify ecological variables on a fine scale, *i.e.* in 0.25m<sup>2</sup> quadrats where plants grow, to test for niche differentiation among species. Third, we analyse the flowering phenology of the six *Lythrum* species to test for temporal differences in relation to (a) each other and (b) the mean and range of flowering time in the local community.

# Materials And Methods

## *Study area and species*

This study was carried out in the Mediterranean region of the South of France. We studied six annual species of the genus *Lythrum* (Tison et al. 2014) that have small flowers that are probably self-pollinated (Gazaix 2019) and are closely related but vary in chromosome number and distribution in the South of France (Table 1; Online resource 1). All known occurrences of the six species in the South of France were extracted from the *Silene* database of the French National Mediterranean Botanical Conservatory of Porquerolles on the 26/03/2018 in order to select populations for study.

**Table 1 Systematics and distribution (maps in Appendix A) of the six studied *Lythrum* species.**

Phylogeny (unpublished data)	Species	Number of chromosomes	Distribution
	<i>L. thesioides</i>	$2n=30^1$	Mediterranean region to central Asia
	<i>L. borysthenicum</i>	$2n=30^2$	Mediterranean region to central Asia
	<i>L. portula</i>	$2n=10^{2,3,4}$	Northern and eastern Europe
	<i>L. hyssopifolia</i>	$n=10^{2,5}$ , $2n=20^6$ , $2n=30^7$	Mediterranean region, Europe, central Asia, invasive in Australia and North America
	<i>L. thymifolia</i>	$n=5^2$ , $2n=10^8$	Mediterranean region to central Asia
	<i>L. tribracteatum</i>	$n=5^2$	Mediterranean region to central Asia

<sup>1</sup> (Gazaix et al. 2019)

<sup>2</sup> (Castroviejo Bolibar et al. 1997)

<sup>3</sup> (Hollingsworth et al. 1992)

<sup>4</sup> (Lökvist and Hultgård 1999)

<sup>5</sup> (Ruíz de Clavijo and García-Panta-León 1986)

<sup>6</sup> (Měsíček and Jarolímová 1992)

<sup>7</sup> (Les 2017)

<sup>8</sup> (Favarger and Galland 1985)

The distribution of Mediterranean temporary pools in the south of France is heterogeneous. In Mediterranean continental France, Médail et al. (1998) recognized 15 determinant temporary pool areas

that can be grouped into three main regions: Mediterranean France east of the Rhône valley, the lower Rhone Valley (Costières, la Capelle and Crau) and finally a range of small areas to the west of the Rhône valley. Our sampling was designed to cover these three regions and to reflect the distribution and abundance of the six annual *Lythrum* species (Fig. 1, Online resource 2). Three populations of *L. hyssopifolia* were sampled in all three regions, three populations of *L. borysthenicum*, *L. thymifolia* and *L. tribacteatum* were sampled in each of two regions, and *L. thesioides* and *L. portula* were sampled in only one region due to their rarity (Gazaix et al. 2019).

### *Spatial co-occurrence*

We compared the spatial co-occurrence of the six species at two different spatial scales: a biogeographical scale (10 km grid) and a microhabitat scale (0.25 m<sup>2</sup> quadrat). Biogeographic analyses are based on point data contained in the *Silene* database, aggregated in a 10 km \*10 km grid. This database contains a very complete inventory of Mediterranean temporary pools in the South of France. We only used data points that have been reported since 2000. For the microhabitat scale, we used community data gathered when sampling niche variables (see below) to assess the local co-occurrence of species.

For each spatial scale, we built a site\*species table where each row is a species, and each column a sampling unit (one grid cell, one quadrat) and values are presence/absence of the taxa. We then calculated a dissimilarity index between columns using Jaccard index, and represented it thanks to a dendrogram. We assessed the uncertainty of each node of the hierarchical clustering based on the bootstrap procedure implemented in the *hclust* function of *pvclust* package with a *binary* option for distance, *average* option for clustering and 10000 bootstraps (Suzuki and Shimodaira 2006).

### *Ecological niche*

We quantified the ecological niche of all taxa following a common protocol that characterises above ground microhabitat structure and soil parameters. For each population, data were collected in five quadrats (50 cm x 50 cm), established at least 1 m apart. Each quadrat contained one hundred contact points in a 5 cm grid. For each point, we recorded contact points with the following elements: moss, lichen, bare soil, rock, gravel (>0.5 cm), litter and living plant species (identified as precisely as possible). If the contact was made with two different components, we attributed a value of 0.5 to each contact. Any other contacts were ignored. Hence, the total cover per quadrat could not exceed 100% allowing the 100 contact points to quantify the frequency of each variable.

Soil was sampled for each quadrat in three microsites to a depth of 5 cm. The soil was dried (40°C, 2 weeks), sieved at 2 mm and conserved before analysis. Following Papuga et al. (2015), after mixing 10 g of dry soil with 20mL of distilled water, we blended the solution for 20 min, separated phases using a centrifuge (10 min), and measured pH and conductivity in the supernatant at room temperature (ca. 20°C), using an Eutech Cyberscan. Then, water-retention capacity was calculated as the percentage of water remaining in previously 40°C dried soil by again drying the sample at 110°C for 5 hours. Organic matter was estimated as the percentage of matter lost after burning a dried sample at 500°C for 5h. The

total amounts of carbon (C) and nitrogen (N) were determined using a ThermoFinnigan Flash EA 1112 series on 70-µg samples grinded with a crusher (3 min, frequency = 30).

Three different groups of variables were defined for each quadrat. First, we computed the number of species and the Shannon index using the diversity function of the *vegan* package (Oksanen et al. 2019), and percentage per quadrat of the different biological growth forms (Raunkiaer 1934): annual (therophytes) and perennial (total, and either phanerophyte, chamephyte, hemicryptophyte and geophyte) following information in Tison et al. (2014). Second we quantified a range of soil variables: (pH, conductivity, carbon and nitrogen content, carbon:nitrogen ratio (C:N), water-retention capacity and organic matter content). Third we quantified abiotic cover variables in terms of the percentage cover of mineral elements (stones, gravel and rock), bare soil, litter and mosses (combined with lichens).

We made a selection of variables within those three groups by analysis of correlations using the *rquery.cormat* function. We only retained variables with  $r < 0.5$ . Principal Component Analysis on combined data was then performed using the *dudi.pca* function of the package *ade4* (Dray and Dufour 2007). Spatial analysis to determine whether each species had different positions for PCA coordinates was based on the function *Adonis* of the package *vegan*. For each variable, glm was run (variable ~ taxon + region, family= Gaussian) and effects due to differences among regions were assessed by an F-test (Bolker et al. 2009). Ranges of values per species were calculated (maximal-minimal value) per variables and standardized between 0 and 1 (the latter corresponding to the maximum value per variable) across the six species.

### *Phenology*

To analyse the phenology of the community in which each species was studied, we drew violin plots based on the mean flowering date of the community of each quadrat, calculated as the median of flowering date of each species modulated by its cover:

$$\left(\frac{1}{N-1} \sum_{i=0}^{N-1} f_i c_i\right).$$

Here,  $f_i$  is the median of the flowering date of the species  $i$ ,  $c_i$  is the cover per quadrat for species  $i$ ,  $N$  is the number of species in the quadrat. The target species were excluded from the analyses ( $N-1$ ) and are shown in the violin plot by lines that represent maximum, minimum and median flowering dates. Information for this analysis was also gathered from Tison et al. (2014). To evaluate the significance of phenological differences among communities associated with different species of *Lythrum*, we ran a Gene Lin Mod (family = Gaussian) with the mean flowering date of communities (one per quadrat) as response variable, and the species of *Lythrum* (Taxon), the area where it was studied (Region) and the date of field sampling (Date) as explanatory variables. Data were analysed using R statistical software version 3.5.1 (R Core Team 2017) with the *ade4* (Dray and Dufour 2007) and *vegan* (Oksanen et al. 2019) packages.

# Results

## Spatial cooccurrence

On a biogeographic scale we detected two main groups of species with very strong statistical support (Fig. 2a), one with *L. hyssopifolia* with *L. tribracteatum* (84 % bootstrap probability), the other with *Lythrum borysthenicum* and *L. thymifolia* (100% bootstrap probability). Those two groups are distinct and root together with *L. portula* forming an overall group separate from *L. thesioides*. On a microhabitat scale (~ 0.25m<sup>2</sup>, Fig. 2b) *L. hyssopifolia* and *L. tribracteatum* group closely together again (65% bootstrap probability) whereas *L. borysthenicum* and *L. thymifolia* form a close group but with less significant probabilities (53% bootstrap probability) and root with *L. portula* (68% bootstrap probability) prior to a rooting with the other pair of species. *L. thesioides* remains separated. In general, at the local scale probabilities are lower, perhaps because of a smaller sample size (n = 158) compared to that used biogeographic analyses (n = 240).

## Micro-ecological niche differentiation

We selected 12 variables for the principal component analysis: (a) three soil parameters: pH, soil carbon content (%), C:N ratio; (b) four abiotic cover variables: stones, bare soil, moss and litter cover; (c) five plant community variables: therophyte, hemicryptophyte, geophyte cover and cumulative phanerophytes + chamaephyte cover, and the Shannon index. Four axes were kept in the analysis, with 21, 16, 13 and 11 % of the total inertia. The examination of the four different axes revealed that only the first two axes proved discrimination of the realised niche space occupied by the different species of *Lythrum*.

The first axis (21%) is primarily explained by variation in therophyte cover, pH and carbon content, and to a lesser extent the C:N ratio and the total cover of phanerophytes and chamaephytes (Fig. 3). This axis discriminated *L. thesioides* and *L. tribracteatum* from *L. hyssopifolia* (with an intermediate position over a wider niche space) and the three remaining species (*L. borysthenicum*, *L. portula* and *L. thymifolia*). The second axis (16%) is mostly explained by carbon content, bare soil and geophyte cover (Fig. 3) and discriminated *L. tribracteatum* from *L. thesioides* and *L. thymifolia*. *Lythrum portula* and *L. borysthenicum* were also slightly separated from *L. thymifolia* and *L. thesioides*, but not from *L. tribracteatum*. Finally, *L. hyssopifolia* shows an intermediate position with a wide range. Comparison of different species with the *adonis* function produced significant differences between all species pairs except *L. portula* – *L. borysthenicum* and *L. portula* – *L. thymifolia*. However, while adjusted and non-adjusted *p*-values are not significant for the former pair, the non-adjusted *p*-value is significant for the latter pair (Online resource 3). However, these results illustrate a lack of niche differentiation between *L. portula* and *L. borysthenicum* for the studied variables.

For individual variables, a clear result is that the six species occur in microhabitats across a range of pH values that shows a graduation of significant differences based on pairwise comparisons (Fig. 4a): *L. borysthenicum* (mean = 5.6 ± 0.6), *L. portula* (5.9 ± 1.2), *L. thymifolia* (6.4 ± 0.56), *L. hyssopifolia* (7 ± 1), *L.*

*tribracteatum* ( $7.5 \pm 0.34$ ) and *L. thesioides* ( $7.8 \pm 0.14$ ). Second for the remaining variables *L. thesioides* and *L. tribracteatum* present particular and unique ecological niche differences while the four other species have less marked differences. *L. tribracteatum* occurs in microsites with a high soil carbon content (Fig. 4b) and a high geophyte cover (Fig. 4f) while *L. thesioides* occurs in microsites with a low cover of therophytes (Fig. 4c) and a high bare soil cover (Fig. 4e) and C:N ratio (Fig. 4d). For the remaining species, few differences occurred for variables other than pH. These differences involve a slightly lower cover of moss in the habitat of *L. borysthenicum* compared with *L. portula* and *L. thymifolia*, and a higher cover of stones in the habitat of *L. thymifolia* relative to *L. borysthenicum* and *L. portula* (Online resource 4).

Finally, the ranges of each species (*i.e.* maximum – minimum values) for the twelve different variables were notably wider for *L. hyssopifolia* for several variables (Fig. 4). *L. tribracteatum* had the widest ranges for carbon content and geophyte and bare soil cover. *L. thymifolia* had a wide range for moss and stones that were mostly observed to have very low values (mean values of 1.8% and 2.5% respectively in all samples). *L. thesioides* had low ranges for most variables except litter, bare soil and phanerophyte cover.

## Phenological variation

Mean flowering time in the communities associated with the six species of *Lythrum* was significantly different (Fig. 5). However, differences were very slight, from the minimum mean value of flowering time in the community that was observed in association with *L. thymifolia* ( $6 \pm 0.75$ ) to the maximum value with *L. portula* ( $6.64 \pm 0.46$ ). Hence significant variation may simply be due to differences between the latter two extreme species. There is however a clear difference among the six *Lythrum* species in their flowering time relative to that of their local community. Whereas *L. thymifolia* has peak flowering that is early relative to that of other species in the community, peak flowering of *L. borysthenicum* is similar to the mean value of the community and peak flowering of *L. hyssopifolia* and *L. tribracteatum* is towards the end of the flowering period of their communities. Finally, *L. portula* and *L. thesioides* have peak flowering later than all other species in their communities and the latter species has a range of flowering time that is later than all other peak values of flowering time in its local community.

## Discussion

Our study revealed marked differences in the ecological niche of six studied annual *Lythrum* species in terms of highly localised spatial variation in ecological parameters and flowering period. Soil conditions contribute to niche differentiation among species, particularly pH. We discuss the implications of this niche differentiation for the spatial distribution and coexistence of the six species and for the conservation management of Mediterranean temporary pools.

## Spatial niche differentiation

The spatial association of the six *Lythrum* species on biogeographic (10km grid cells) and highly localized (small 0,25m<sup>2</sup> quadrats within populations) scales show marked similarities with two main groups of coexistence, one of which varies depending on spatial scale due to a difference concerning the position of *L. portula*. This species has a continental distribution area (Online resource 1) and is rare in the Mediterranean region (Tison et al. 2014), where it co-occurs with all other species on a biogeographic scale but more closely with *L. borysthenicum* and *L. thymifolia* on a localized ecological niche scale. Its ecological niche is thus more similar to that of *L. borysthenicum*, and *L. thymifolia*, whereas it occurs less often in the same biogeographic grid cells with these species, causing its different position in the two cluster analyses. Indeed, the observed variation among species in the PCA analyses of niche variables is more similar to their position in the cluster analysis of presence in small quadrats than with presence in 10km grid cells. This is the first indication from our study that the local scale is highly pertinent for the evaluation of differences in the ecological niche within this genus, and probably temporary pool species in general. *L. hyssopifolia* is one of the most common species of annual *Lythrum* and it shows an ecological overlap with all the other species and was found in association with all other species. The study of the micro-niche revealed marked differentiation among species in their ecological niche on a fine scale. In addition to hydrology, an important driver of plant distribution in temporary pools (Jeffries 2008; Rhazi et al. 2009; Caria et al. 2013; Minissale and Sciandrello 2016) and niche differentiation (Silvertown 2004; Emery et al. 2012; Silvertown et al. 2015; Auderset Joye and Boissezon 2018), our study provides strong evidence of niche differentiation among species in relation to edaphic parameters. Although *L. portula* and *L. borysthenicum* showed only low levels of variation in ecological conditions between each other, they showed marked differentiation from the other species in our study. Two main factors distinguish the position of the different species along gradients of variation in soil parameters.

The first is pH, a factor that has a major influence on plant distribution (Sims 1986; Gough et al. 2000; Chytrý et al. 2010) and plant diversity in Mediterranean temporary pools (Caria et al. 2013). For the six species of annual *Lythrum*, two species show a wide tolerance of pH, two species are restricted to limestone substrates to the west of the Rhône valley and two species have a preference for acidic substrates in Provence (notably in the Maures). Second, our results identify an association of some species with carbon content and the C:N ratio, two soil parameters that are important drivers in plant distribution (Luo et al. 2017) and niche differences on other Mediterranean-type habitats (Lavergne et al. 2004; Papuga et al. 2018). In particular, the presence of *L. tribracteatum* is associated with a high soil carbon content and high soil conductivity (that was not used in the PCA analysis because of high correlation with carbon content), a result that illustrates that this species could tolerate salinity. The C:N ratio is higher for *L. thesioides* than any other species. These results are probably linked to differences in the hydrology of the temporary pool habitat; carbon content is known to be higher in temporary pools flooded for a longer period (Sahuquillo et al. 2012).

Vegetation composition is less associated with differences in the niche of the six species, no doubt because annual species are the most common groups of species in nearly all samples. Indeed, this life history strategy is the dominant type in Mediterranean temporary pools (Médail et al. 1998; Bagella and Caria 2012). The only differences in vegetation composition concern a higher geophyte cover in

microhabitats of *L. tribracteatum*, mostly due to the presence of *Aeluropus littoralis* and *Bolboschoenus maritimus* that are typical of brackish ecosystems in the Mediterranean region. *L. thesioides* is found where total vegetation cover is low in two artificial pits – the species was only recently discovered at this site following soil excavations for architectural remains (Gazaix et al. 2019). The micro-habitat of this species at this site is in fact on the steep of the pits and their slope is so rapid that even within the small quadrats hemicryptophyte species that are not typical temporary pool species (they occur at higher levels that surround Mediterranean temporary pools) are present. This is another indication of the fundamental need to analyze niche variation on a highly localized scale where plants grow.

## Phenological niche differences

The flowering period is well known to influence niche differentiation among closely related species (Levin 2009), a pattern that has also been observed in wetland plant communities (Bell and Clarke 2004; Auderset Joye and Boissezon 2018). Our index of the flowering period of the communities of the different *Lythrum* species showed only slight differences among the six species of *Lythrum*, although differences were low and poorly significant in pairwise comparisons. This is due to the wide range of variation in flowering time for communities in which these annual species occur.

There were however marked differences in variation in peak flowering time of the six *Lythrum* species in relation to the mean and range of flowering time in their local community. These observations are based on observed dates of flowering in the regional flora (Tison et al. 2014) and may thus mask inter-annual variability in years of low spring rainfall and local variability; hence some prudence is required in their interpretation. Peak flowering of *L. thymifolia* is early relative to other species and that of *L. borysthenicum* is similar to the mean value of the community. In contrast peak flowering of the four other species is late, or much later relative to that of their community. Indeed, the two species that are biogeographically and ecologically distinct from the others, *L. portula* and *L. thesioides*, have peak flowering that is clearly later than all other species in their communities. What is more, the latter species has a range of flowering time that is later than all other peak values of flowering time in its local community. Although the low variation in flowering time of *L. thesioides* may be due to its rarity, the later flowering time relative to the local community indicates that both species do not have the typical flowering phenology of Mediterranean temporary pool species, as their global distributions would also suggest (Supplementary Information Fig. 1). As seen in the analysis of niche parameters above these two species show much divergence in their ecology and coexistence with other species that run parallel with these differences in phenology.

The variation in the flowering time of the six studied species may also follow hydrological gradients in the Mediterranean temporary pools where they occur (Rocarpin et al. 2015; Valdez et al. 2019). Comparisons of the germination phenology of *L. thymifolia*, *L. borysthenicum*, *L. thesioides* and *L. tribracteatum* illustrate that the two former species germinate at lower temperature than the latter two species (Gazaix 2019). This difference fits their differences in flowering phenology. Indeed, a main driver of phenology may be the germination niche (Grubb 1977) especially in Mediterranean temporary pools due to the short life cycle of the majority of species that are present (Médail et al. 1998; Rhazi et al.

2009). Our study lacks any information on differences in depth within the pools (*i.e.* a proxy of the hydrological gradient), but this feature has been reported to be important for niche differentiation among *Lasthenia* (Asteraceae) species in Californian vernal pools (Emery et al. 2012).

## Possible phylogenetic niche conservatism?

Niche conservatism under phylogenetical constraints is well known in higher plants (Prinzing et al. 2001; Wood et al. 2009). In addition to information on the coexistence and specialization of annual plant species in Mediterranean temporary pools, our study has pertinence for understanding how niche differentiation may be related to evolutionary divergence. The phylogenetic position of the six *Lythrum* species has recently been described (A. Gazaix, unpublished manuscript) and is shown in Table 1. The comparison with our results for ecological similarity and differentiation has pertinence for understanding their role in the evolutionary divergence of this group of closely related species.

First, *L. thesioides* remains distinct from other species, genetically, biographically and in terms of its ecology. Second, *L. portula* and *L. borysthenicum* occur in a distinct clade and have very similar ecological niches, particularly in terms of soil variables (Fig. 3) and cluster analyses (biogeographic and quadrat scales). This clade represents a major historical divergence of these two species on acidic soils relative to those on limestone (ancestral *L. thesioides* and recently diverged *L. hyssopifolia* and *L. tribracteatum* occur on limestone). However, the subsequent divergence of these two species on acidic substrates from each other is associated with marked conservatism in their ecological niche. Third, *L. hyssopifolia* and *L. tribracteatum* occur in the second clade that is associated with conservatism in terms of pH and occurrence over a wide range of ecological variation, albeit with a higher C:N ratio and carbon content for *L. tribracteatum*. There is thus evidence for both niche conservatism during historical and recent phylogenetic diversification and also occasional divergence in relation to niche expansion into different ecological conditions. These results bear similarities with a recent study of rapid divergence of the genus *Lasthenia* in temporary pools in California (Emery et al. 2012). They reported that although large-scale climate axes have been highly labile during the history of the genus, the microhabitat involving position on local depth gradients has been relatively conserved among lineages, either because close relatives in *Lasthenia* rarely occur in sympatry and thus may not have occasioned divergent selection for microhabitat conditions or because of competitive exclusion and phylogenetic evenness within local communities.

Evolution in the genus *Lythrum* may also be associated with changes in ploidy level, a common feature of divergence in flowering plants (Wood et al. 2009; Thompson 2020). In *Lythrum*, while the ancestral number for the genus is supposed to be  $2n = 10$  (Graham and Cavalcanti 2001), which occurs in *L. thymifolia*, *L. portula* and *L. tribracteatum*, the three other species have different chromosome counts and ploidy levels. *L. borysthenicum* and *L. thesioides* are triploids, and *L. hyssopifolia* is diploid or triploid according to different sources (Table 1). Polyploidization may thus be associated with ancestral divergence of *L. thesioides*, more recent divergence of *L. borysthenicum* and *L. portula* (species that showed low levels of ecological differentiation in our study), and the wide ecological and biogeographic range of *L. hyssopifolia*.

# Insights for conservation

Our study clearly shows that *Lythrum thesioides* is by far the most distinct species, in terms of its biogeographic associations, ecology and phylogenetic position and also its rarity. We now know that this species can show dramatically long periods of dormancy and appear furtively when ecological conditions are favorable (Gazaix et al. 2019). Although this rarity may contribute to some of the results it nevertheless illustrates an important association between rarity and uniqueness that, in the current absence of more information on the ecology of this species, should be used as an argument for its recognition as a priority species for conservation.

Our study provides information for the restoration of Mediterranean temporary pools for this species and its congeners. Indeed, the importance of correctly identifying the ecological requirements of rare species for the success of reintroduction programs has been clearly identified (Fiedler and Laven 1996; Godefroid et al. 2010; Adhikari et al. 2012). In addition, some Mediterranean temporary pools are considered as priority habitats for conservation under the European Habitats Directive which contains four different temporary pool community-type in France (Bensettiti et al. 2005). Our results illustrate that this classification is too simple for conservation management of individual rare species – there is marked ecological differentiation among the six *Lythrum* species that are typical of this habitat. Conservation management should thus take into account micro-spatial variation within this habitat, i.e. the scale on which coexistence of different species occurs. Maintaining such local spatial diversity in ecological conditions would enhance the ability of the flora of Mediterranean temporary pools to persist in landscapes where this habitat has dramatically declined in the last 50 years (Zacharias and Zamparas 2010).

Finally, alongside the studies of Lavergne et al. (2004) and Papuga et al. (2018), and other examples in Mediterranean plant species (Thompson 2020), *Lythrum* provides an example of the importance of fine-scaled ecological differences in the ecological niche of different populations or related species within the context of a single broad-habitat unit, i.e. temporary wetlands. The scale of such niche differentiation is thus particularly important to take into account for the conservation management of Mediterranean temporary pools.

## Declarations

**Supplementary information** Additional supporting information may be found online version of the article

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**Ethics approval** Not applicable

**Consent for publication** All authors have given their consent for the publication of this manuscript

**Consent to participate** All authors have given their consent to participate to this manuscript

**Data availability** The dataset used and analyzed during the current study are available from the corresponding authors on reasonable request.

**Authors' contributions** AG, GP, PGrillas, PGauthier and JT conceived and designed the experiment. AG, GP, PGauthier, VP, HF and FS performed the fieldwork. AG, GP and HF analyzed the data. AG, GP, PGrillas, PGauthier and JT wrote the manuscript.

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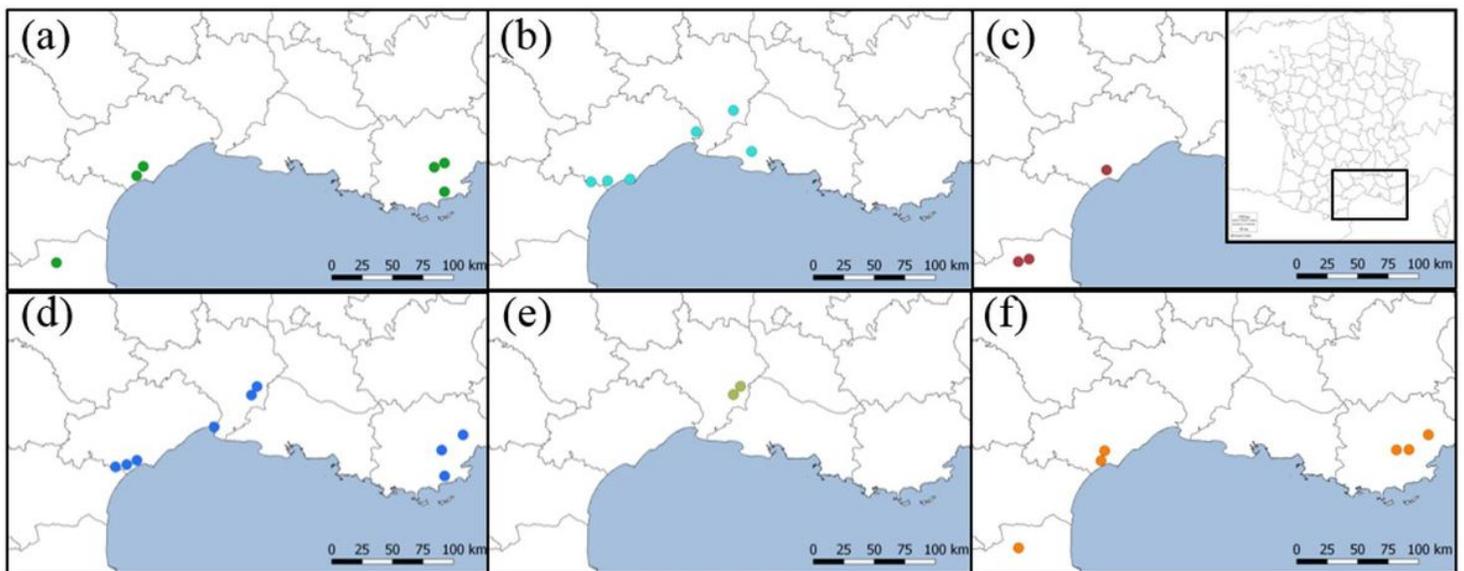
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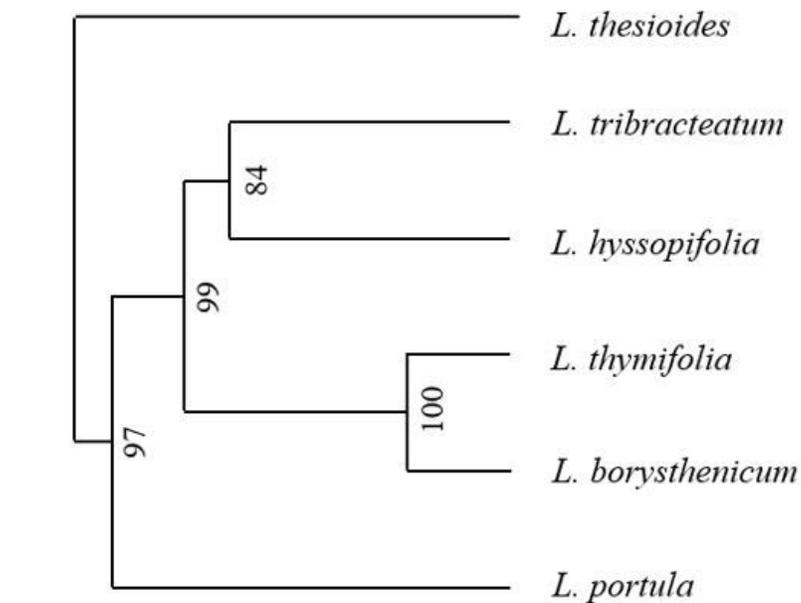
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## Figures

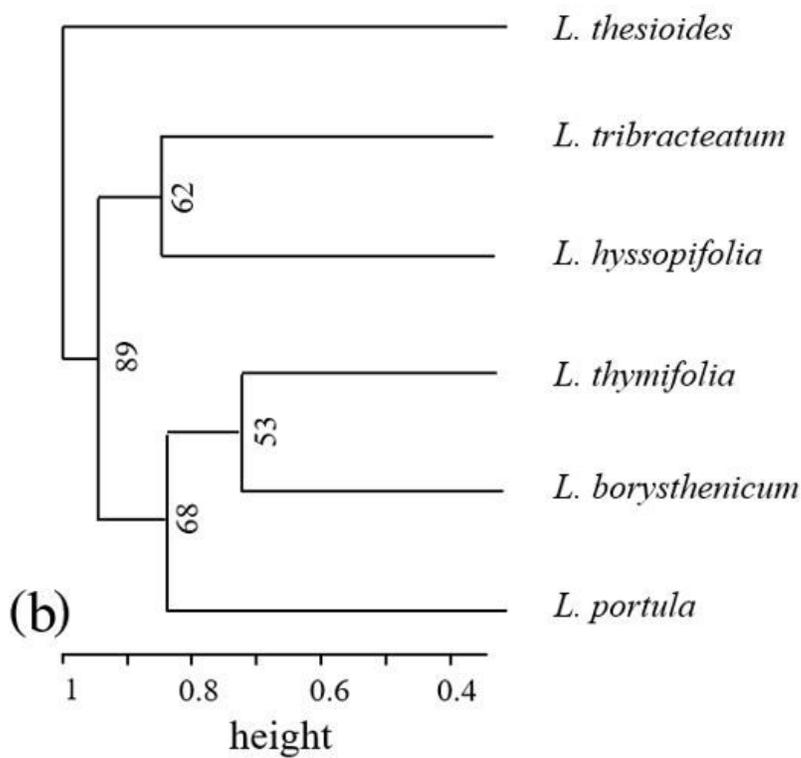


**Figure 1**

Sampled sites for the six species of *Lythrum* in the South of France: a) *L. borysthenicum*, b) *L. tribracteatum*, c) *L. portula*, d) *L. hyssopifolia*, e) *L. thesioides*, f) *L. thymifolia*. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.



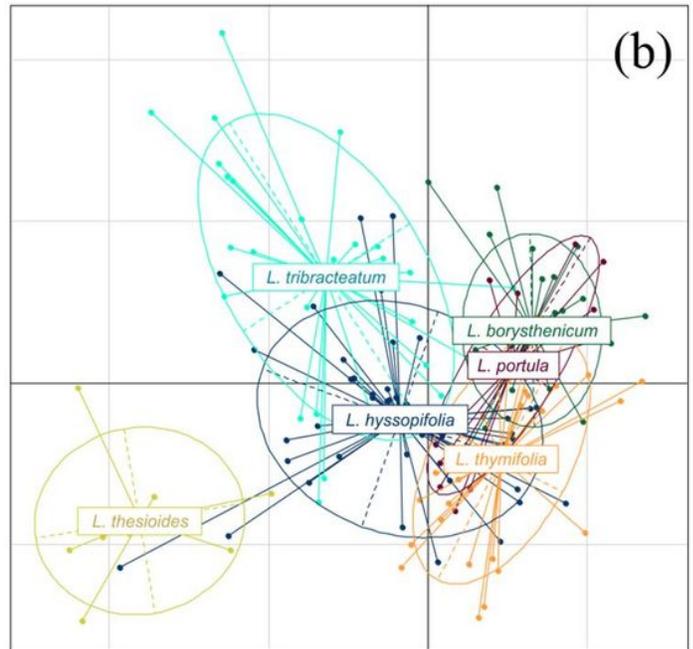
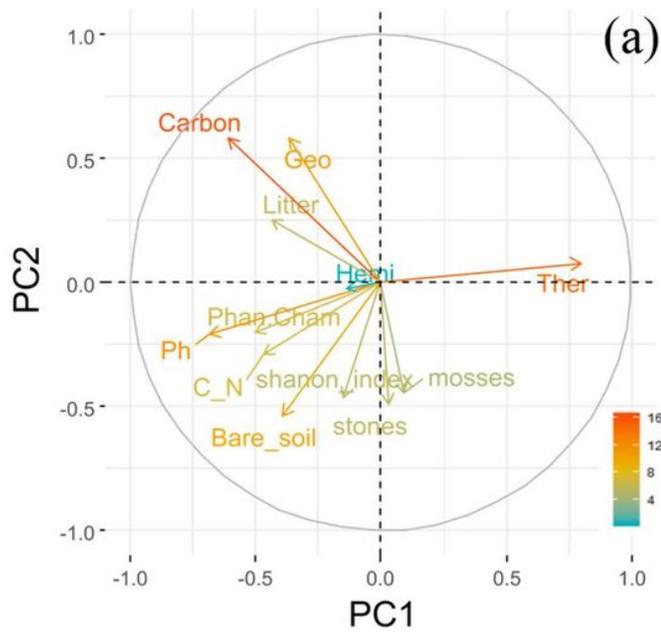
(a)



(b)

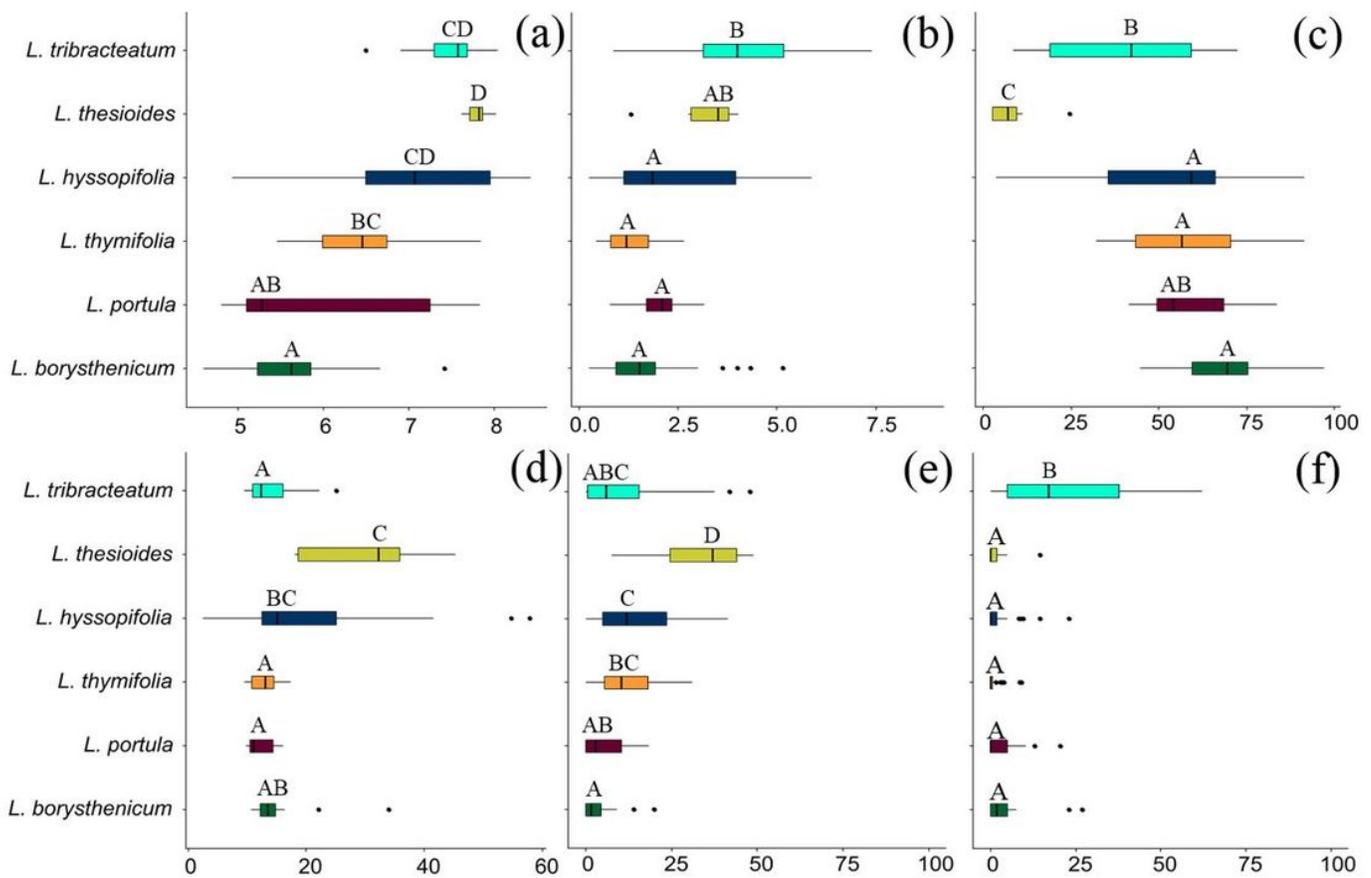
**Figure 2**

Cluster analyses for the coexistence of the six species of *Lythrum* on two spatial scales in the South of France: a) 10 km grid squares (n=240) and b) 0.25 m<sup>2</sup> quadrats within populations (n=158). Values below nodes correspond to bootstrap probabilities calculated by the pvclust function.



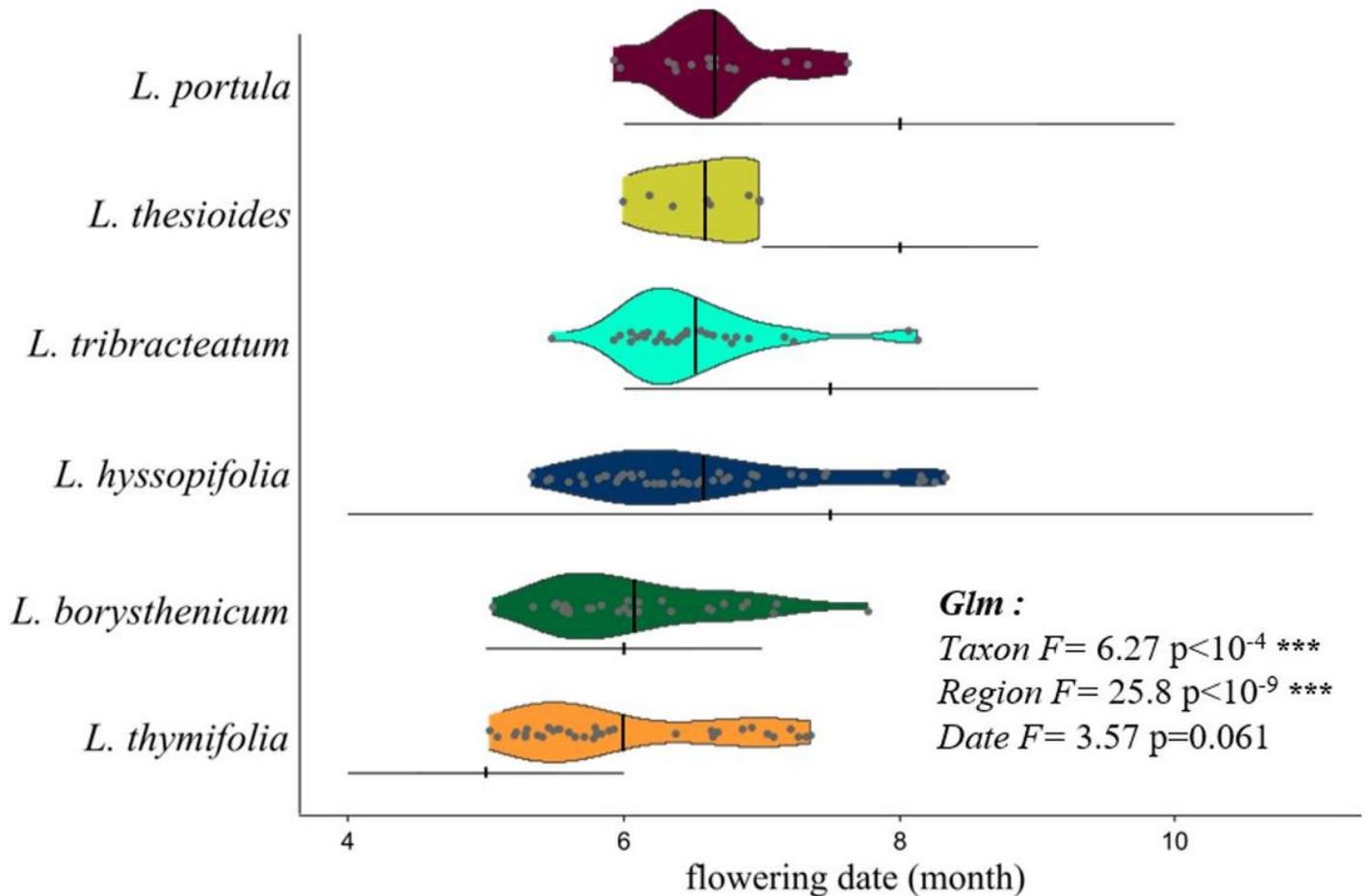
**Figure 3**

Results of principal component analysis. a) The carbon / nitrogen ratio (C\_N) and the cover of geophytes (Geo), hemicryptophytes (Hemi), therophytes (Ther), and phanerophytes + chamephytes (Phan.Cham) on the first two axes. b) Quadrats of each species on the first two axes (PC1: 21 % and PC2: 16 %).



**Figure 4**

Mean and range of six ecological variables that show significant differences among the studied Lythrum species: a) pH, b) soil carbon content (%), c) therophyte cover (%), d) carbon : nitrogen ratio, e) bare soil (%), f) geophyte cover (%). Groups of significance from post-hoc Tukey tests among species are presented (A different code letter represents a significant difference from species with other code letters for a given variable).



**Figure 5**

Mean flowering time (black vertical lines) and periods for communities associated with the sampled quadrats (dots) for each species of *Lythrum*. We draw Kernel density estimations for each species. Horizontal lines represent the blooming period of each *Lythrum* species with the vertical trait representing the median. Phenology data are from Tison et al. (2014). Glm indication gives the values of the F-test for the model per variable, with associated p-values.

## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

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