NÖVÉNYI INVÁZIÓ KÉRDÉSEINEK VIZSGÁLATA FELSZÍNI VIZEKBEN

NKFI-KH 129520 sz. OTKA pályázat

Szakmai zárójelentés

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Kutatási eredmények

A KH OTKA pályázatot egy kimagasló idézettségű közleményre alapozva pályáztam, két évig futott, ami két fő tudományos munkatárs teljes idejű alkalmazását tette lehetővé.

A pályázatban a vízinövényeket érintő biológiai invázió eddig kevésbé vizsgált aspektusait, kérdéseit igyekeztünk, megvizsgálni: (i) ellenállóbbak e az idegenhonos fajok a herbivóriával szemben és (ii) befolyásolja e egy élőhely funkcionális diverzitása az idegenhonos fajok megtelepedésének sikerességét? Ezek a kérdések az ezzel párhuzamosan futó FK-OTKA (127939) pályázatomat szorosan kiegészítik. A tervezett kutatás kiinduló pontja, hogy az ökológiában széles körben alkalmazott klasszikusnak is mondott niche elmélet (HUTCHINSON 1959) sok esetben nem elégséges a biológiai invázióval kapcsolatos kérdések magyarázatára. Sok esetben tapasztalható, hogy nagyon átfedő nich-el rendelkező idegenhonos fajok is képesek egymás mellett élni, ami szembe megy a niche elmélettel. Ezért ebben a kutatásban más alternatív hipotéziseket (enemy release és diverzitás) tesztelünk.

A pályázat időtartama 2 év volt (2018. 10 – 2020.09), ebben az időperiódusban kellett a szintén 2018-ban induló FK OTKA pályázatot is indítani. A két pályázat annyiban átfedett, hogy a herbivóriás kísérletekhez is szükséges mezokozmosz rendszert az FK OTKA pályázatból fedezve építettem ki. Mindkét pályázat megvalósítását késleltette, hogy a beruházás a tervezettnél kicsit lassabban valósult meg a szokásos (árajánlatok, közbeszerzés és kivitelezés) csúszások miatt. Ez kb 5 hónap csúszást okozott a kísérletek kezdésében. A pályázat második évében a COVID 19 járvány igen jelentős akadályt jelentett a pályázat során. Itt a home-office miatt az adatok értékelésének üteme lett sokkal lassabb, részben e maitt is módosult kissé az első vizsgálati kérdés.

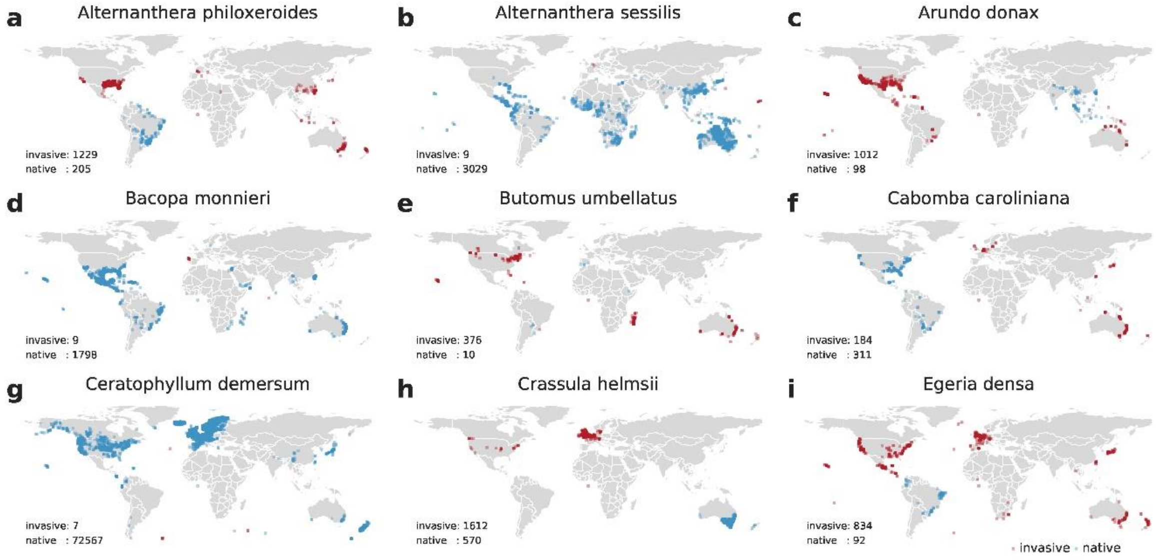
A pályázatban két fő kérdéskört terveztünk vizsgálni. (i) A pályázatban eredetileg az élőhelyek faji- és funkcionális diverzitásának az invázió sikerességére gyakorolt hatását terveztük vizsgálni. Azonban egy lehetőséget kihasználva kissé más irányba vittük el a kutatást. Ez jelentősen megkönnyítette a munkát, az eredeti terveknek megfelelő vizsgálathoz házon belül is szorosabb együttműködés kellett volna, illetve sokkal több külföldi partnerrel kellet volna együtt dolgozni, ami a 2020 eleji karantén miatt nagyon nehezen let volna kivitelezhető. Ugyanakkor rendelkezésre állt egy adatbázis, amo szintén nemzetközi kooperácóban készült. A GBIF és TRY adatbázisokból nyert adatok alapján készítettünk egy olyan globális léptékű elemzést amely a növényi jellegek szerepét vizsgálja az inváziós sikerében, kölön elemezve a terresztris és vízi növényeket. Ezt 2019-2020-ban végeztük. (ii) 2020-ban a herbivória szerepét vizsgáltuk egy laboratóriumi kísérlet során. Alábbiakban ennek a két kérdésnek a mentén ismertetem a pályázatban elvégzett vizsgálatok eredményeit:

1. Funkcionális diverzitás vizsgálat

A biológia invázió sikerességét számos tényező képes befolyásolni. A sikert befolyásolja az élőhelyek állapota, zavartságának a mértéke, de hatással vannak rá az élőhelyen található őshonos és az újonnan érkező idegenhonos fajok képességei, belső tulajdonságai is. Ez utóbbaikat összefoglaló néven funkcionális jellegeknek hívjuk. Azt biztosan tudjuk, hogy bizonyos jellegek előnyt jelentenek az invázió során, ilyen pl. a gyors növekedési ráta, vagy az allelopatikus anyagok termelésének képessége. Előnyös jellegek birtokában egyes fajok gyorsabban terjednek, gyorsabban alkalmazkodnak új környezetben vagy a kompetíció során helyzeti előnyhöz jutnak más fajokal szemben. A növényökológia ezen ráészének viszonlag széleskörű irodalma van. A fajok jellegeinek ismerete alapján kockázati becsléseket is végezhetünk, ez fontos eszköz a védekezés tekintetében. A funkcionális jellegek tehát segíthenek bennünket az ilyen típusú kockázat elemzésben. Az inváziós növényfajoknak a jellegeik alapján történő osztályozása, kockázati besorolására, illetve magunkak az inváziós jellegeknek a meghatározására sok irodalmi adat áll rendelkezésre. Az eredmények többségének lokális léptéke miatt azonban sok esetben egymásnak ellentmondó eredményeket szolgáltatnak, amit cask a nagyobb léptékű elemzésekkel lehet feloldani. Az elérhető globális jelleg és biotikai adatbázisok megjelenésével elkezdődtek az ilyen globális léptékű elemzések is.

Az általunk végzet ilyen globális léptékű vizsgálatban 48 vízi és 280 terresztris idegenhonos növényfaj mintegy 48 653 rekordján keresztül elemeztük hét növényi jelleg szerepét az invázió sikerében. Az invázió sikerét a rekordok száma alapján határoztuk meg 0-1-2 kategóriákba sorolva a fajokat. A fajokhoz a jelleg adatokat a TRY adatbázisból vettük. Az elemzéshez a WorldClim adatbázisból klimatikus adatokat is felhasználtunk, mint az elterjedést potenciálisan meghatározó változók. A környezeti változók, a jelleg adatok és a biotikai adatok asszociáltságának együttes értékeléséhez az RLQ és fourth-corner elemzést használtuk.

A Mann-Whitney elemzés alapján az inváziós vízi és terresztris növényfajok a hajtáshosszban ($U = 1824.5$, $p < 0.001$, Figure 1a), levelek száraz tömegében ($U = 613$, $p < 0.001$, Figure 1b) mutattak szignifikáns különbséget. Az elvégzett Kruskal-Wallis teszt alapján a jellegek közül az alacsonyabb hajtáshossz ($\chi2 = 19.46$, $p < 0.001$, Figure 2a), a nagyobb specifikus levélfelület ($\chi2 = 7.60$, $p = 0.022$, Figure 2b), a kisebb levélfelület ($\chi2 = 18.11$, $p < 0.001$, Figure 2c), és a növekedési forma ($\chi2 = 15.13$, $p < 0.001$) előnyösnek bizonyult az invázió sikerssége szempontjából, érdekes módon a mag jellegek egyike sem bizonyultak meghatározó jellegnek holott ezt az irodalom alapján várni lehetett volna. A filogenetikai kontroll mellett (PGLS) alkalmazott Bayesian-féle általánosított lineáris modell is a specifikus levélfelületet, a növények növekedési formáját, a hajtásmagasságot és az adott területen mérhető éves átlagos csapadék mennyiségét adta a legfontosabb tényezőkenek ami egy invázió sikerességét meghatározhatja. A RLQ és fourth-corner együttes elemzés azonban csak a növény típusa (vízi-terrszetris), a növekedési forma, hajtáshossz valamint a hőmérséklet és szezonalitás alacsonyabb értékei között mutatott ki negatív korrlációt. Az eredmények értékelése és elemzése még tart. A kézirat első verzióját készítettük el (lásd 1. melléklet). **Az eredmények előzetes elemzése alapján a vizsgálatunk egyik fő mondanivalója az lehet, hogy a globális léptékben nézve a biológiai invázió nem egy sztochasztikus folyamat, mint azt korábban sokan leírták, hanem jól prediktálható a környezeti változók és növényi jellegek együttes elemzése alapján. Másik irányvonal ami felé az eredményeink diszkusszálása folyik, és ami ellentmond a legfrissebb nemzetközi inváziós eredményeknek, hogy a növények hajtáshossza igenis egy meghatározó tényező a sikeresség szempontjából.** Természetesen az adatok értelmezése és diszkusszálása még folyamatban van. Az adatsor nagysága és a bogográfiai lefedettség miatt a mi kutatásunk egy nagyon robosztus elemzésnek mondható, ez alapján egy erősebb tudomáynis folyóratban szeretnénk megjelentetni.



1. ábra. Néhány példa a globális elemzéshez használt GBIF fajadatok léptékéről.

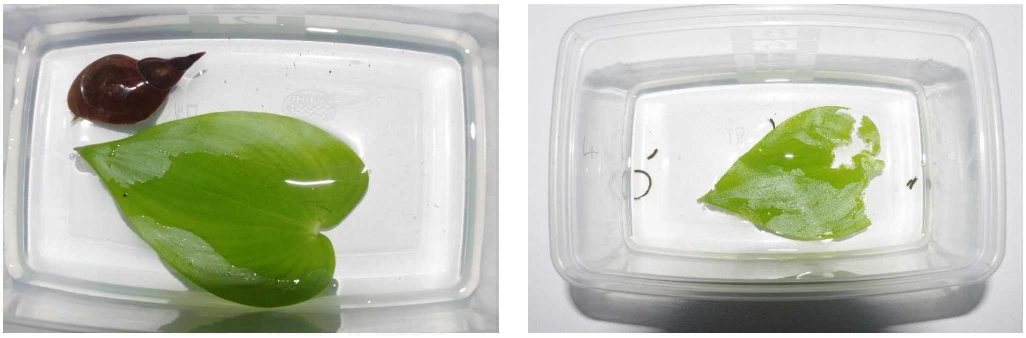
2. Herbivória kísérlet

Természetes élőhelyén minden növényfajt érint valamilyen mértékben a herbivória. A növényevő állatok a legelés során adott helyen, kisebb-nagyobb mértékben de visszafogják a növények primer produkcióját, ezáltal befolyásolva a növényfajok közötti kompetíciót. Ez ellen a növények képesek védekezni is (mechanikai úton vagy allelopathikus vegyületek segítségével). Az egyik legismertebb inváziós hipotézis, a természetes ellenségektől történő megszabadulás hipotézis (enemy release hypotheses) szerint a biológiai invázió során egy új élőhelyre bekerülő inváziós faj számára kompetíciós előnyt jelent, hogy részben vagy akár teljesen is mentesül az eredeti élőhelyén jellemző, az ő életfeltételeit alapvetően befolyásoló ellenségektől. Az ellenségek alatt itt minden olyan élőlényt kell érteni ami az ő fitnesszét csökkenti (betegségeket, kártevők, legelő állatok stb). Ennek oka, hogy ezek az ellenségek nem vagy csak később követik az invázió során magukat az inváziós fajokat, az új élőhelyen meglevő hasonló “ellenségek” ismeretlen faj révén eleinte kerülik azt. Ezt számos vizsgálatban igazolták már terrszetris növényfajokon.

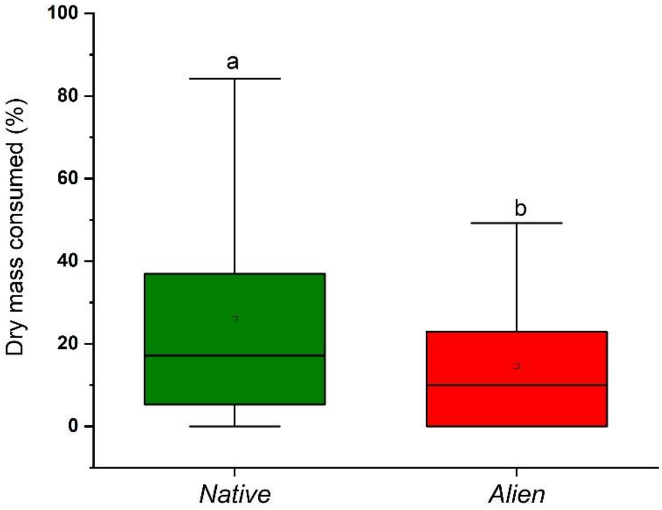
Az általunk végzett kutatás során 33 vízinövény fajt (14 idegenhonos, 19 őshonos) vontunk kísérletbe, ezek között voltak valódi hinarak (n=20) és mocsári növények (n=13) is. A filogenetikai rokonságból következő lehetséges hibát úgy igyekeztünk kizárni, hogy a bevont fajok a lehető legtávolabbi rokonok legyenek. A generalista herbivór állatként a nagy mocsárcsigát (*Lymnaea stagnalis*) választottuk, mert minden típusú vízben megtalálható, könnyen begyűjthető és nem “válogatós”. Az etetéses kísérletek során a begyűjtött fajok leveleit (n=10) sötétben tartva etettük a csigákkal 24 órán keresztül. A kísérlet során a herbivória mértékét az elfogyasztott szárazanyag tömeggel fejeztük ki, követve Elger & Wilby (2000) munkáját. A kutatás alapkérdései: (i) A herbivória mértékében van e különbség a honos és idegenhonos hínárnövények között? (ii) Vizsgáltuk, hogy van e összefüggés a levelek szárazanyag tartalma és a fogyaszthatósága között? (Lehet e általános következtetéseket levonni a herbivóriával kapcsolatban a könnyen mérhető levél szárazanyag tartalom adatokból?)

A kapott eredményeket általánosított kevert modellekkel és variancia nalízissel is értékeltük. A kevert modellek esetében az az elfogyasztott szárazanyag tartalom értékek (mint függő változó) és az őshonos-idegenhonos jelleg (mint független változó) összefüggését vizsgáltuk, ahol a fajnév és a csiga tömege mint random faktor szerepeltek. A GLMM és ANOVA elemzések eredményei alapján a honos és idegenhonos fajok fogyaszthatósága szignifikánsan eltért, az őshonos fajokat nagyobb arányban fogyasztották (1. és 2. ábra). A csiga súlya és taxonómiai hovatartozása nem befolyásolta az eredményeket. **Ez alapján a természetes ellenségektől történő megszabadulás hipotézis (enemy release hipotézis) a hínárnövények esetében is egyértelműen igazolható. A vizsgálat másik feltételezése, miszerint a levelek alacsonyabb szárazanyag tartalma növeli a levelek fogyaszthatóságát szintén igazolható** (R^2=0.52), a korreláció erőssége az idegenhonos fajok esetében nagyobb (R^2=0.65) (3. ábra). Így a levél szárazanyag tartalom (LDMC) jelleg a herbivóriával szembeni ellenáló képesség kifejezéséhez is, mint általános összefüggés alkalmazható.

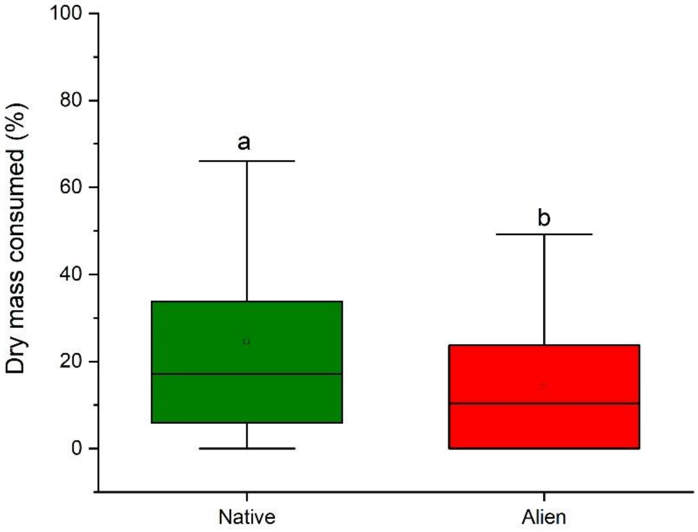
A vízi növények esetében csak egy vizsgálatról tudunk (Xiong et al. 2008) ami ugyenezt a kérdést kutatta. Ebben kutatásban 8 kínában őshonos és 8 idegenhonos növényfaj bevonásával vizsgálták vagyis jóva kevesebb fajt vizsgáltak. Ugyanakkor a kínai vizsgálatban a mintaszám és a fajkészlet elég torznak volt mondható, 16 növényfajt vizsgáltak ezek közül 8 a Hydrocharitaceae családba tartozott, vagyis a filogenetikai rokonságból eredő hiba nem volt kiküszöbölve.



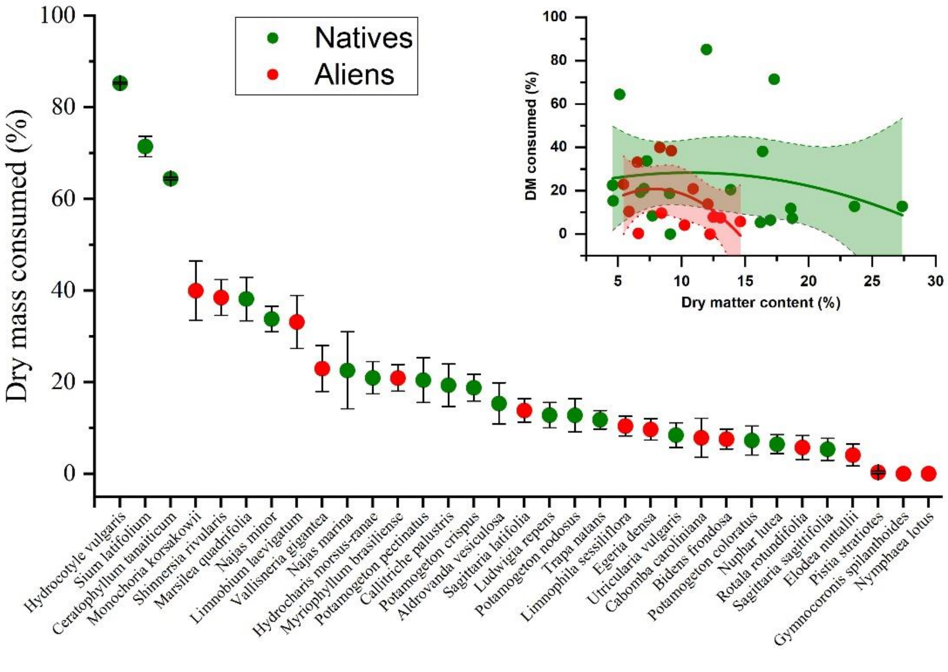
1. ábra. A kísérletben a fenti képhez hasonló módon egy nagy mocsárcsiga (*Lymnaea stagnalis*) mellé helyeztünk egy levelet (itt kék rizsjácint - *Monochoria korsakowii*). Látható a levél a kísérlet indításakor (bal oldali kép) és 24 óra elteltével (jobb oldali kép).



2. ábra. Az elfogyasztott szárazanyagtartalom a honos és idegenhonos hínár- és mocsári növényfajok esetében. Az eltérő betűk a honos és idegnehono sfajok közötti szignfikáns különséget mutatják (ANOVA).



3. ábra. Az elfogyasztott szárazanyagtartalom a honos és idegenhonos hínárnövény fajok esetében. Az eltérő betűk a honos és idegnehono sfajok közötti szignfikáns különséget mutatják (ANOVA).



4. ábra. A kísérlet során az egyes növényfajokon mért elfogyasztott szárazanyagtartalom értékek. Mellék ábra: Az elfogyasztott szárazanyag tartalom és a levelek szárazanyagtartalma közötti összefüggés a honos és idegenhonos fajok között.

Publikációk

A pályázat ideje alatt számos tudományos cikket írtam angol nyelven, a pályázatban megfogalmazott konkrét célokhoz azonban azok csak részben kapcsolódnak, sokkal inkább a párhuamosan futó FK OTKA eredményeit összegzik. A pályázatban vállalt két kutatási témából egy kézirat verzió (mellékletben csatolva) már elkészült, a másikat pedig éppen elkezdjük írni. Ezek benyújtása a következő egy-másfél évben várható.

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Dr. Lukács Balázs András

Comparing invasion success of aquatic and terrestrial plant species: a trait based study

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Abstract: xxxxxxx

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Introduction

Invasions of alien plant species negatively impact the ecosystems worldwide. Introducing new plant species to suitable habitats in the case of the success of the newly introduced species can completely change the habitat structure (xxx), and can negatively affect the native species diversity (xxx), mainly due to the high competitive ability of alien plants caused by different characteristics of alien plants compared to native ones (xxx). When different conditions allow, selected plant species become superabundant in their introduced ranges, as they must own at least some highly successful characteristics, which let them spread in their introduced ranges. Although the result is the extreme abuncance of some species, there might be several different reasons responsible for success, like empty niches, or dominated coexistence by the invaders of the same niche in the introduced range (MacDougall et al. 2009); a biotic resistance to plant invasions can be provided by native herbivores in their native range which cannot be provided in the conquered regions (Parker et al. 2006); while "novel weapons" can be also developed in occupied territories what native populations otherwise lack at their original range (Callaway & Ridenour 2004). While all of these hypothesises require further comparative biogeographical approaches, the importance of trait-based approaches is also constantly growing in invasion biology to identify the most important factors responsible for invasion success of both terrestrial and aquatic alien plant species.

Analysing the risks in plant invasions significantly evolved in community ecology in the past few decades. In order to predict invasion success, a huge variety of life history traits are available for us. Several trait based studies were published recently which attempted to analyse the features that separate successful invaders from failing ones (e.g. Simberloff et al. 2013, Van Kleunen et al. 2010). For instance, many studies proved that invasive species seems to be larger and have higher growth rate than species that are not invasive among terrestrial plants (van Kleunen et al. 2010), and a huge variety of studies revealed that specific leaf area (SLA) and seed mass are also very important traits for successful invasions (Hamilton et al. 2005, Dawson et al. 2009); however, successful invasions can be also related even with floral traits (Gibson et al. 2012), or indirectly, the pollen vectors (Küster et al. 2008). According to Pyšek & Richardson (2008), beside the often subjected testing of such traits as plant height or clonality, flowering time seems to be also very important (see also Crawley et al. 1996, or Cadotte & Lovett-Doust 2001), as early flowering and/or extended flowering period provide advantage for invaders in the competition with native ones. Havel et al. (2015) suggested that the most common successful invaders will include those that can reach new freshwater environments while also those that have great abilities for asexual breeding, high reproductive output, generalist feeding, or broad environmental tolerance; while they also suggest that the most successful ones include more than two of these characteristics. Among others, the importance of phenology (the timing of periodic life-history events) is also inevitably important, and can also lead us to key results in evaluating the success of invasive species (Wolkovich & Cleland 2011).

While identifying some key traits in success sometimes seems easy, it also seems that reliably identifying the most relevant functional traits which are representative of differences in plant invasions are sometimes rather hard, furthermore it also complicates the situation that different traits potentially have a different impact on invasion success on different stages of the invasion (Kolar & Lodge 2001, Pyšek et al. 2003). Novel frameworks also emphasise that an approach of predicting plant invasions should consider the prevailing environmental conditions using mostly climatic data, and the traits of both resident and native species (Moles et al. 2008). In their study, Funk et al. (2017) also suggested that efforts on understanding critical traits should be focused as fully as possible both on biotic and abiotic context to develop new models which account the key interactions in a given system, especially across trophic levels (see also Deraison et al. 2015, or Lavorel et al. 2013). This statement can be truly important as the primer thoughts about the better ability of alien plants in profiting more from high resource supply were shaded by recent studies. For instance, according to a meta-analysis, high-resource environments do not specifically cause aliens to outperform natives in carbon capture, thus aliens and natives benefits the same from increased resource availability (Ordonez & Olff 2013). This has been further supported by Leishman et al. (2007): they found that although alien plants do not have fundamentally different carbon capture strategies from natives, but species with specific leaf traits enabling rapid development will be successful invaders when introduced to environments mainly where resources are not that limited as at their native ranges. The role of leaf traits has been also showed in the study of Lukács et al. (2017), where the authors have suggested that the trait-based approach of autochthony can apply to aquatic environments similar to terrestrial ones, and leaf traits have a great relevance in explaining aquatic plant ecology whether traits are combined with growth-forms as a fixed factor. Their results also confirmed the importance of traits related to competitive ability in the process of aquatic plant invasions. These results can be important as freshwater ecosystems and wetlands may be the most endangered ecosystems in the world, yet they are still highly exposed to animal and plant invasions; however, the exposition on them significantly differs, as while nutrient rich tropical freshwaters are among one the most threatened habitats by invasive organisms, a very low level of invasions on peatlands can be observed (Chytrý et al. 2009).

Brundu (2015) suggested that the lack of a common framework for assessing the risks posed by invasive alien aquatic species is seen as a key gap in Europe. Successful management should include several key tasks, like habitat restoration, prevention, and also prioritization both in prohibiting activity about alien species, and setting new paths in researching risks about potential invasions in the future. Moreover, Pyšek & Richardson (2008) emphasised the relevance of studies in a wider geographical scale, as studies at a single spatial scale are unlikely to discern the drivers of invasion patterns (as shown by Collingham et al. 2000), and the effect of a given trait may differ at various scales (e.g. Hamilton et al. 2005; Lloret et al. 2005).

In a world where acceleration of numerous invasions in nature harms most of the ecosystems, the need for studying alien plants in their introduced and native range seems essential for many reasons (Hierro et al. 2005). Although trait-based approaches are becoming more popular worldwide, according to our best knowledge, no studies were published in comparing the distribution of native and alien species in a worldwide survey by using abundance data, and finding the key traits responsible for the success of alien plants using both single-trait and multi-trait analysis. In their study, Divisek et al. (2008) evaluated the similarity of introduced plant species to native ones by comparing native and alien species. They found that although the first "defence line" of habitats against alien species is environmental filtering, major differences in trait comparing to native ones significantly enhanced invasion success and the ability to occupy novel niche spaces including on the edge of trait space. Despite the authors have conducted both a single-trait and multi-trait analyses, and they used two kind of approach to calculate trait data for species having no trait values in the database, they used traits in their study without using abundance data of the studied species.

As public trait databases are completely suitable for conducting multi-trait analysis, we aimed to perform a comprehensive study in analysing the key differences in life history traits of aquatic and terrestrial invasive species, and identify traits that might play a key role in invasion success by using abundance data of these species. Our questions were: i) does successful invasive aquatic and terrestrial species differs in their traits ii) which traits promote or help naturalization and dispersion iii) does tropical and temperate species have differences (within aquatic and terrestrial separately) in their invasion strategy, do they possess different trait strategy? Our hypotheses were: (1) alien aquatic plants differ from terrestrial plants in the vast majority of their life history traits (2) regarding leaf economic traits, it is predictable that successful invasive species have higher specific leaf area, lower leaf dry matter content and higher leaf nitrogen content than less successful alien species (3) life-form and growth-form tends to be relevant in the comparison of aquatic and terrestrial alien species (4) the seed mass of more successful species to be lower, regardless of whether it is aquatic or terrestrial.

Materials and methods

Data collection

We collected data for 48 aquatic and 290 terrestrial alien species from TRY database (Kattge et al. 2011a, b). A total of 48,653 records was used to define 7 trait predictors. Plant growth form contained hydrophyte, graminoid, herbaceous, shrub, tree and epiphyte. We assigned numbers 1-6 for these categories, respectively, for the analyses. Plant height in metre (m), seed length in millimetre (mm), seed dry mass in milligram (mg), leaf dry mass in gram (g), leaf area in square millimetre (mm^2) and specific leaf area in square millimetre per milligram (mm^2*mg^{-1}) were averaged. Before the analyses, plant height, seed dry mass and leaf area were log-transformed at the natural base to rescale extremely outlier data points.

Taxonomic information (family) and the biogeographic origin of species were checked in online databases (http://www.theplantlist.org/, https://pfaf.org/). Spatial data (coordinates) for species presence as invasive were collected from XXX database. Climatic data were downloaded from the WorldClim database (https://worldclim.org/data/bioclim.html) for a total of 3,790,580 (684,430 invasive and 3,106,150 native) occurrences. We averaged the climatic variables per species for further analyses and also searched the corresponding country for each coordinate.

Based on the number of records per invasive species, we classified the level of success as follows: 0 – low level of success when the number of records is lower or equal to the first quartile value, 1 – medium level of success when the number of records is higher than the first quartile value but lower or equal to the third quartile value, and 2 – high level of success when the number of records is higher than the third quartile value. However, some of the methods used during the analyses required binary encoding of the response variable, therefore, we applied the same classification using the median value as cutting point (0 – low level of success, 1 – high level of success).

Statistical analyses

Environmental data were available for nineteen bioclimatic variables from which we used five temperature (BIO1-BIO4, BIO7) and four precipitation (BIO12-BIO15) variables that contained the relevant climatic information for our study. First, we reduced this high number of climatic factors by applying principal component analysis (Hotelling 1933). Only the first two PCs, which explained 81.93% of the total variation were extracted and used in further analyses. PC.tempe represented temperature (higher values of temperature seasonality with higher values of temperature annual range), whilst PC.prec was highly contributed by two precipitation related variables (higher values of precipitation seasonality with lower values of precipitation of the driest month).

The Mann-Whitney test (Mann & Whitney 1947) was used to identify differences in the values of each trait of aquatic and terrestrial species. Similarly, the Kruskal-Wallis test (Kruskal & Wallis 1952) was applied on the three levels of success and Dunn's test (Dunn 1964) was used to check differences among the groups.

We used a Bayesian generalized linear mixed model (Bayesian GLMM, Hadfield 2010) approache to evaluate the associations between multiple predictors and the response variable. In a first set of models, plant type (aquatic or terrestrial) was the response variable and the taxonomic relationships (family and genus:family) and the origin of species were the random factors. In a second set of models, the level of success (low or high) was the response variable and we also included plant type as a fourth random factor in each models. We applied binomial error distribution for model fitting. We used a standard set of priors for the Bayesian models (Hadfield 2019) and allowed them to run 600,000-5,000,000 iterations with a 10 to

20% burn-in and a thinning interval between 54-1500 in order to achieve sufficiently high (>1000) effective sample sizes for the estimated parameters.

Furthermore, we used the phylogenetic generalized least squares (PGLS, Symonds & Blomberg 2014) approach for controlling the phylogenetic relationships of species. This method estimates the expected covariance and hence modifies the parameters according to the assumption that closely related species have more likely similar traits. We estimated best-fitted values of the phylogenetic signal (Pagel's λ, Pagel 1997, 1999) from likelihood-profiles for each model (Kamilar & Cooper 2013). In this analysis, we included 117 species that were available on a previously published phylogenetic tree (Durka & Michalski 2012).

We performed model selection for all possible models for all of the approaches described above. The models were ranked by the Deviance Information Criterion (DIC) of Bayesian GLMMs and Akaike's Information Criterion corrected for small sample sizes (AICc) of PGLS models. A subset of models ($\Delta < 2$) were used for averaging parameters and calculating variable importance values after reweighting the selected models (Burnham & Anderson 2002, Symonds & Moussalli 2011). We checked also the interactions among all predictors (Spearman 1904) to reveal possible correlations among predictors during multi-model inference.

Finally, we used an integrative approach for evaluating trait-envrionment interactions. A combination of RLQ anf fourth-corner methods were chosen for this purspose (e.g. Dray et al. 2014, Baattrup-Pedersen et al. 2016). These methods allow to simultaneously analyse the information in three tables: R (*n* x *m*, including *m* environmental variables for n sites), L (*n* x *p*, implying the abundance or occurrence of *p* species at *n* sites), and Q (*p* x *s*, containing data on *s* traits for *p* species). The RLQ anlysis provides a global summary of the scores assigned to species, sites, traits and environmental variables, whilst the fourth-corner approach tests multiple associations among traits and environmental variables (Dray et al. 2014). The countries, previously determined by mapping the coordinates of occurences, were given the *n* sites for tables R and L. The most complex model type that permutes on the values of both sites and species were used. The number of permutations was set to 50,000.

All predictors were centred and scaled before the comparative analyses. Data processing, Mann-Whitney and Kruskal-Wallis tests were performed in R v3.6.0 (R Core Team 2019). The functions available in the packages 'dunn.test' for Dunn's test (Dinno 2017), 'MCMCglmm' for Bayesian GLMM (Hadfield 2010), 'nlme' for PGLS (Pinheiro et al. 2019), 'AICcmodavg' for parameter averaging (Mazerolle 2019) and 'ade4' for RLQ and fourth-corner analyses (Dray & Dufour 2007) were also used during the analyses.

Results

Interactions among predictors

Many of the predictors had high correlation with other predictors (Table 1). Therefore, we excluded seed length, leaf dry mass and leaf area from multi-model inference, however, we present the results of the tests on the comparison of species groups also including these predictors.

Differences between aquatic and terrestrial species

According to the results of Mann-Whitney tests, aquatic species are substantially different from terrestrial species in height ($U = 1824.5$, $p < 0.001$, Figure 1a), leaf dry mass ($U = 613$, $p < 0.001$, Figure 1b), PC.prec ($U = 4563$, $p = 0.019$, Figure 1c), growth form ($U = 1243.5$, $p < 0.001$) and almost significantly in PC.temp ($U = 7001$, $p = 0.054$, Figure 1d) but not in seed dry mass ($U = 2423.5$, $p = 0.062$, Figure 1e), seed length ($U = 380$, $p = 0.97$, Figure 1f), specific leaf area ($U = 1359$, $p = 0.141$, Figure 1g) and also not in leaf area ($U = 1930$, $p = 0.226$, Figure

1h). Model selections revealed that the most important predictors associated with plant type are growth form, height and to a lesser extent specific leaf area and seed dry mass (Table 2).

Furthermore, aquatic and terrestrial species are not different in the level of success (Kruskal-Wallis test, $\chi^2 = 3.66$, $p = 0.161$; Bayesian GLMM, posterior mean = 12.12, $p = 0.108$; PGLS, $\beta = 0.04$, $t_{117} = 1.52$, $p = 0.132$), and therefore, we included all species in further comparisons and the categories of aquatic and terrestrial as random factors during the model selection procedure for Bayesian GLMM.

Contribution of factors to the success of alien species

The Kruskal-Wallis tests showed differences among the levels of success in height ($\chi^2 = 19.46$, $p < 0.001$, Figure 2a), specific leaf area ($\chi^2 = 7.60$, $p = 0.022$, Figure 2b), leaf area ($\chi^2 = 18.11$, $p < 0.001$, Figure 2c), PC.temp ($\chi^2 = 46.63$, $p < 0.001$, Figure 2d), growth form ($\chi^2 = 15.13$, $p < 0.001$) and in PC.prec ($\chi^2 = 9.11$, $p = 0.011$, Figure 2e) but not in seed dry mass ($\chi^2 = 5.13$, $p = 0.077$, Figure 2f), seed length ($\chi^2 = 2.44$, $p = 0.295$, Figure 2g) and also not in leaf dry mass ($\chi^2 = 1.21$, $p = 0.545$, Figure 2h).

Applying Dunn's test on predictors showing significant results in Kruskal-Wallis tests showed that species with high level of success significantly differ in height from species with low level of success ($Z = -3.88$, $p < 0.001$) and also from medium level of success ($Z = -3.68$, $p < 0.001$). For specific leaf area, species with high level of success only differ from species with medium level of success ($Z = 2.67$, $p = 0.011$), however, for leaf area, species with low level of success significantly differ from species with high ($Z = -4.19$, $p < 0.001$) and medium level of success ($Z = 3.43$, $p < 0.001$). For PC.temp, all groups are significantly different (low to high, $Z = 6.67$, $p < 0.001$; medium to high, $Z = 5.05$, $p < 0.001$; medium to low, $Z = -2.64$, $p = 0.004$), however, for PC.prec, species with low level of success significantly differ from species with high ($Z = 2.45$, $p = 0.011$) and medium level of success ($Z = -2.85$, $p = 0.007$). Finally, species with high level of success significantly differ in growth form compared to species with low level of success ($Z = -3.38$, $p < 0.001$) and also to medium level of success ($Z = -3.52$, $p < 0.001$). Speific leaf area, growth form, height and PC.prec showed the highest importance valuses based on the model selections (Table 3).

Trait-environment associations

The first two RLQ axes summarize the relationships between traits and environmental predictors (Table 4) that explains 94% and 2% of the total variance. For the environmental variables, the first axis is mainly described by larger values of annual mean temperature, mean diurnal range and isothermality, whilst the second axis is contributed by lower values of temperature annual range and seasonality (Figure 3a). For traits, the first RLQ axis is characterized by aquatic, less woody plants (likely hydrophyte, graminoid, herbaceous) and lower values of plant height, whereas the second axis differentiates lower seed dry mass and higher specific leaf area (Figure 3b). The fourth-corner analysis alone did not show any significant bivariate association, however, according to the combined RLQ and fourth-corner approach, plant type (aquatic or terrestrial), growth form, and height are negatively associated with the first RLQ axis of environmental factors.

Discussion

Species traits that enhance the ability of species to invade can be separated to two subsets: the first suite is responsible for reaching new habitats mainly by their excellent dispersal traits, while the second one is responsible for succeeding in the new habitat. While dispersal ecology can explain how different organisms can effectively travel to novel suitable habitats, trait based approaches can explain the most relevant characteristics in the success of potential invaders of various habitats. It is unfortunately a widely stated view that climate change will grow the number of opportunities of alien species to invade new areas and habitats (Thuiller et al. 2008), while luckily increased efforts of invasion studies follow this process, and trait-based studies still represent relatively new ways to approach this very complex topic, in order to understand the main invasion processes, even worldwide.

It is obvious that aquatic and terrestrial plants follow completely different strategies during their life history, therefore, our hypotheses was that aquatic and terrestrial species differ in most of their traits. Despite our expectations, this hypothesis was not completely confirmed in this study, as they have significant differences only in height, and leaf dry mass of the totally evaluated six variables. Terrestric invasional plants are taller than aquatic ones, and their leaf dry mass is also higher; however, limited sprout length can be mostly adaptive for emergent aquatic plants, and the latter difference can be easily explained with the fact that most of the aquatic plants try to reach the upper regions of water bodies, where their photosynthesis can be more effective, and where lower leaf mass can help the leaves to float on the water.

Based on the applied model selection, height, growth form, specific leaf area, and the used environmental predictors are the most important influencing factors in the success level of alien species (Table 3). An interesting result of present study was that lower height of alien plants was strongly related to higher invasion success. At first sight, this seems completely the opposite of several comparative trait-based studies about plants based on large species numbers, which were published in the past few decades, as several studies (e.g. Crawley et al. 1996, Williamson & Fitter 1996, Goodwin et al. 1999) reported that plant height was positively related to invasion success, where invasional plants were significantly higher than native ones. However, the explanation of this apparently contradicitonal result can be that these studies compared alien species versus natives, not alien species versus alien species, like it was performed in present study; moreover, Pyšek & Richardson (2008) also highlighted that recent sophisticated studies which evaluated height found no relationship between height and invasiveness (e.g. Hamilton et al. 2005; Lloret et al. 2005; Cadotte et al. 2006), and also mentioned that according to (Thébaud & Simberloff 2001) aliens also do not seem to be generally taller in their invasive ranges. Based on our study, taller plants are less successful in invasion wordwide; and as most of the published invasion studies were geographically restricted, we suggest that future studies conducted in wider ranges and using abundance data of several species would sophisticate the preconception of plant invasion studies which suggest that plant height is generally related to invasion success.

Growth form xxxxx

In our study, for specific leaf area, species with high level of success differ from species with medium level of success. This results is in accordance with studies about the role of higher SLA in invasion success (e.g. Hamilton et al. 2005, Lake & Leishman 2004). Pyšek & Richardson (2008) also suggested that SLA seems to be one of most robust indicators/predictors of invasiveness, as high SLA is also correlated with short leaf retention and fast growth rate.

It seems that despite to former studies, invasions are not entirely random events (Crawley et al. 1996), while understanding the key climate elements responsible for invasion success are also crucial. In our study, the fourth-corner analysis alone did not show any significant bivariate association, but the combined RLQ and fourth-corner approach showed that growth form, and height were negatively associated with the first RLQ axis of environmental factors, where the first axis of environmental variables represents larger values of annual mean temperature, mean diurnal range, and isothermality. In Spain, Pino et al. (2005) showed that the PC most correlated with alien plant species richness and percentage was mainly characterized by latitude, mean temperature, and mean annual rainfall. Although we could not confirm the role of precipitation, or geographic relatedness in plant invasion success in a much wider geographic scale, it seems that only temperature related environmental factors play a key role in plant invasion success worldwide, but according to these results, contradictory not by supporting taller plants in their invasion stages, but by generally limiting plant height, and therefore letting shorter plants to spread more in areas with suitable climate conditions. Although plant height is a very important aspect of the ecology of a species, selection towards greater height depends on how much benefit is to be obtained in the future (Falster & Westoby 2003), and this is obviously also true in the case of any plant invasion of the world, therefore, we suggest that shorter plants with lower need of annual mean temperature, mean diurnal range, and isothermality may globally archieve success imperceptibly, while despite that these results based on a huge dataset of alien plant occurrence, we still suggest that climatic effects are obviously largely modulated by other variables at finer scales.

A common assumption that invasive species occur in higher densities in their introduced range, however, this observation often lacks quantitative data (Hierro et al. 2005). It has been found that the invasional possibilities of many plants in their introduced range are strongly limited by various environmental factors and traits of the given plant (xxx), while beside the explaining traits, the time passed by since the initial introduction is also very important: Pyšek & Richardson (2008) suggest that traits responsible for different stages of invasions should be analysed in the future with increased efforts, in order to avoid introducing biases in multispecies comparison studies, also because different species were introduced in different times, and they are in different stages on the way of naturalization.

Pyšek & Richardson (2008) also suggested that the role of plant traits in the invasion process is to a very large extent stage- and habitat-specific; therefore, habitat need of invasional plants represents also an issue which can nowadays investigated by combining different new approaches. For instance, Pyšek et al. (2010) in their Europe wide study compared terrestrial and freshwater habitats invaded by plants, insects, and vertebrates, and found contrasting patterns in habitat needs, as they found two ecologically distinct groups of alien species (plants and insects versus vertebrates) with strikingly different habitat affinities. Urban and cultivated habitats harboured on average the most alien plants, while highest species densities were also found in these two habitat types in contrast with vertebrates which reached their highest invasion success in woodland, riparian, aquatic and cultivated habitats. This study confirmed that habitat is a major determinant of the level of invasion as shown previously for plants; probably a further global study using abundance data, but taking into account the habitat type of each record would refine our view about plant invasions. Probably further multivariate studies combining different approaches, and which also deal with abundance data, could inform us more objectively about the cumulative success of invasive species, if their occupied habitat types would also be included in the analyses.

Adaptation of invasive plants to new habitats can be also an issue during their spread, where habitat management play a key role in affecting invasive plants. Based on the study of Gross et al. (2015), although native and invasive species differ significantly in their traits, they still had similar responses to grazing and competition mainly because different trait combinations generated similar success to these factors. This firstly suggests that trait differences can underlie also in several coexistence processes even worldwide, and secondly that a variety of used traits in the evaluation can help not just choosing the ones responsible for success, but the ones responsible for success via the stabilized coexistence with native species under certain pressure of local factors.

As local factors include a huge variety of possible biotic and abiotic impacts on the success of invasive species, at most of the times, we are unable to precisely set in order the emerging challenges in management of differently sensitive habitats. Successful management of invasive plants requires several approaches, which can complement each other (Rejmánek 2000); however, it is sure, that although terrestrial habitats have a strong potential to regeneration even after decades of the habitat transformation, the radical transformation of aquatic habitats including the spread of invasional plants in these habitats is a great challenge for us. According to the review of Havel et al. (2015), the most important challenges of the future of handling aquatic invasion plants include the completely new introductions and accelerated dispersal caused by various human behaviours (including the phenomenon of invasion meltdown), the growing level of disturbance in natural or non-natural habitats, or the combined impacts of multiple invasive species. We suggest that management and control methods of invasive alien freshwater species include experimental approaches of dispersal methods (Lovas-Kiss et al. 2020) prevention of spreding by analysing different pathways (xxx), early detection (xxx), while biological and chemical control is also necessary in latter stages (Hussner et al. 2017); according to all of these, the commonplace that prevention is the best defense is still valid in the case of the fight against invasive plants.

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Table 1. Interactions among predictors. **Bold** indicates significant correlations. ρ – Spearman correlation coefficient

Variables	ρ	p
Leaf area ~ Leaf dry mass	0.0534	0.562
Leaf area ~ PC.prec	-0.0669	0.368
Leaf area ~ PC.temp	**-0.2027**	**0.006**
Leaf area ~ Growth form	**0.2752**	**<0.001**
Leaf area ~ Height	**0.4503**	**<0.001**
Leaf area ~ Seed dry mass	**0.1972**	**0.012**
Leaf area ~ Seed length	**0.3856**	**0.001**
Leaf area ~ Specific leaf area	-0.0027	0.975
Leaf dry mass ~ PC.prec	0.0033	0.972
Leaf dry mass ~ PC.temp	-0.0922	0.314
Leaf dry mass ~ Growth form	**0.4579**	**<0.001**
Leaf dry mass ~ Height	**0.5313**	**<0.001**
Leaf dry mass ~ Seed dry mass	**0.2918**	**0.002**
Leaf dry mass ~ Seed length	0.0385	0.761
Leaf dry mass ~ Specific leaf area	**-0.5257**	**<0.001**
PC.prec ~ PC.temp	-0.0782	0.157
PC.prec ~ Growth form	0.0877	0.112
PC.prec ~ Height	0.0024	0.971
PC.prec ~ Seed dry mass	**0.1975**	**0.002**
PC.prec ~ Seed length	0.0934	0.445
PC.prec ~ Specific leaf area	-0.1187	0.155
PC.temp ~ Growth form	**-0.3034**	**<0.001**
PC.temp ~ Height	**-0.3226**	**<0.001**
PC.temp ~ Seed dry mass	**-0.1664**	**0.009**
PC.temp ~ Seed length	0.0181	0.883
PC.temp ~ Specific leaf area	**0.2535**	**0.002**
Growth form ~ Height	**0.7397**	**<0.001**
Growth form ~ Seed dry mass	**0.4236**	**<0.001**
Growth form ~ Seed length	**0.2992**	**0.013**
Growth form ~ Specific leaf area	**-0.3051**	**<0.001**
Height ~ Seed dry mass	**0.4908**	**<0.001**
Height ~ Seed length	**0.5509**	**<0.001**
Height ~ Specific leaf area	**-0.423**	**<0.001**
Seed dry mass ~ Seed length	**0.771**	**<0.001**
Seed dry mass ~ Specific leaf area	**-0.2586**	**0.003**
Seed length ~ Specific leaf area	-0.1237	0.347

Table 2. Differences between aquatic and terrestrial species traits. Average parameter (β), standard error (SE) and variable importance (I) values based on model selection with plant type as response variable. Models with $\Delta < 2$ were used for averaging the values. **Bold** indicates variables that are significant in a single model including that variable alone.

	Bayesian GLMM		PGLS		
Variable	Posterior mean	I	β	SE	I
Specific leaf area	6.9752	0.74	0.0055	0.006	0.29
Height	-0.253	0.69	-0.1203	0.0327	1
Seed dry mass	-2.7074	0.62	not selected		
Growth form	**76.1265**	**0.55**	**0.2439**	**0.0465**	**1**
PC.prec	15.1313	0.53	0.0116	0.0071	0.59
PC.temp	-2.715	0.53	0.0148	0.0086	0.63

Table 3. Life-history traits responsible for invasion success. Average parameter (β), standard error (SE) and variable importance (I) values based on model selection with the level of success as response variable. Models with Δ < 2 were used for averaging the values. **Bold** indicates variables that are significant in a single model including that variable alone. PGLS2 – the level of success was binary, PGLS3 – the level of success was encoded into three categories

	Bayesian GLMM		PGLS2			PGLS3		
Variable	Posterior mean	I	β	SE	I	β	SE	I
Specific leaf area	**31.0963**	**0.98**	0.0194	0.0143	0.32	**0.1132**	**0.0574**	**0.82**
Height	**-24.9448**	**0.59**	-0.1638	0.0627	1	-0.1711	0.0786	0.8
Seed dry mass	-3.478	0.58	0.0039	0.0067	0.14	0.005	0.0062	0.09
PC.temp	**45.2443**	**0.56**	0.0048	0.0068	0.16	0.0303	0.0214	0.32
Growth form	**4.6308**	**0.54**	**0.2412**	**0.0636**	**1**	0.2132	0.084	0.92
PC.prec	18.9024	0.54	**0.1201**	**0.0439**	**1**	**0.109**	**0.0565**	**0.83**

Table 4. Summary of the RLQ analysis.

	Axis 1	Axis 2
Eigenvalues	0.1656	0.0074
% of total co-inertia	94.38	4.19
Covariance	0.407	0.0857
Correlation	0.1447	0.06
Cummulative inertia for environment	4.4251	6.5829
Cummulative inertica for traits	1.7869	2.739

Figure 1a

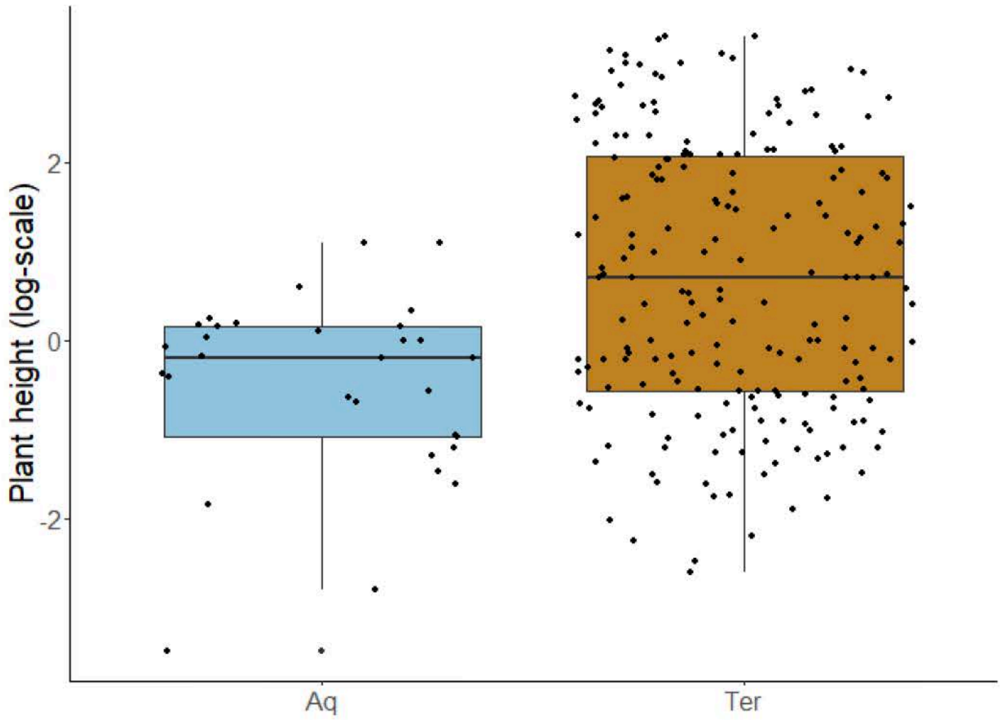


Figure 1b

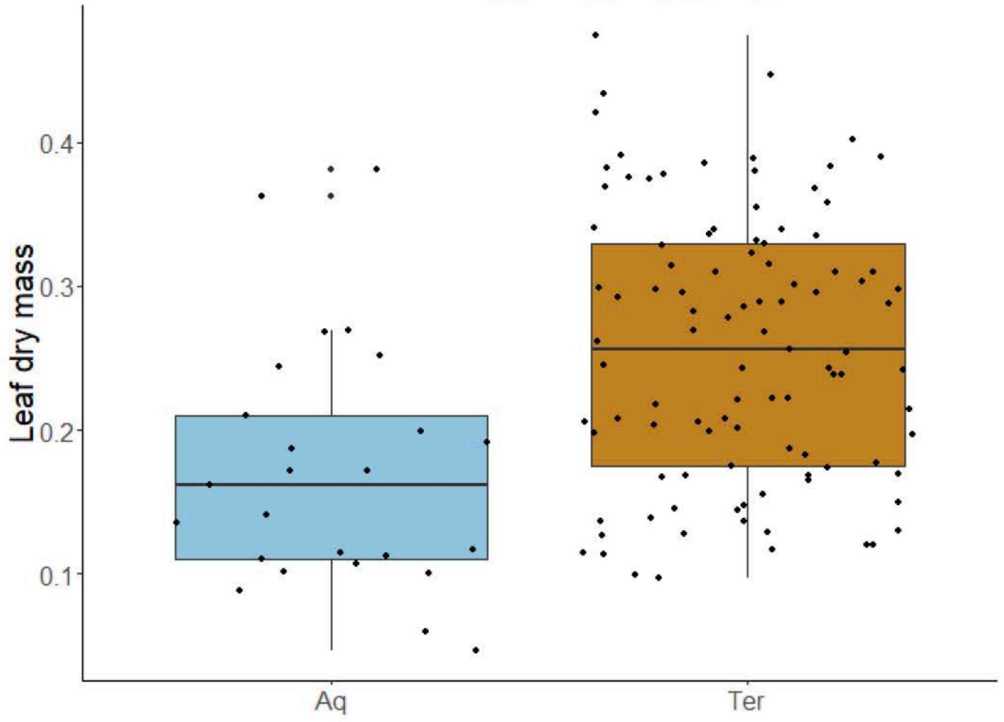


Figure 1c

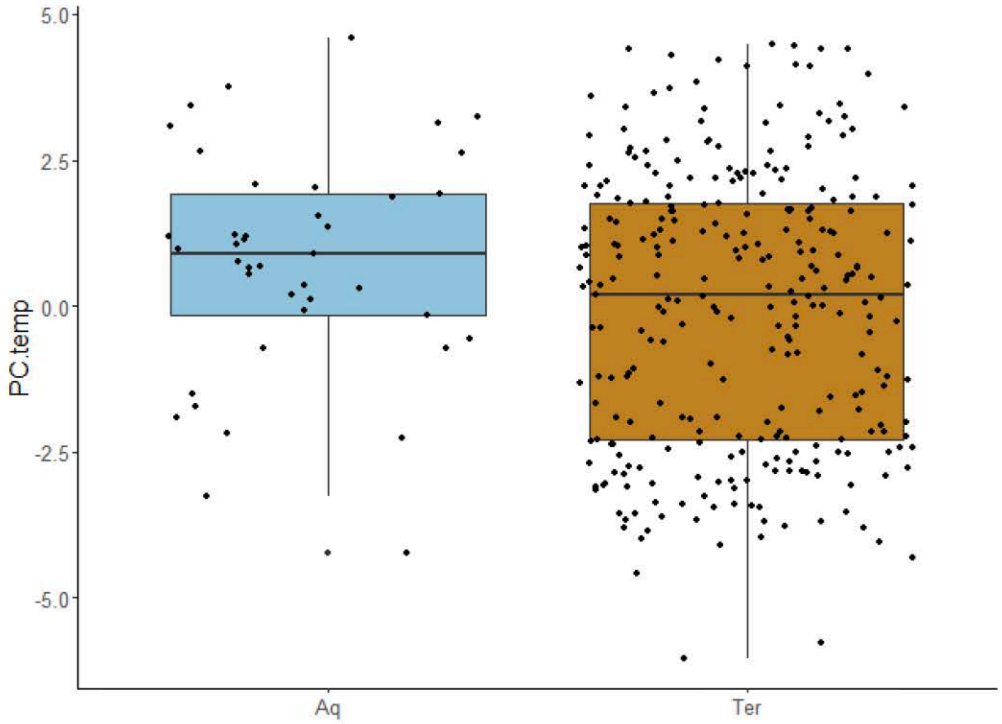
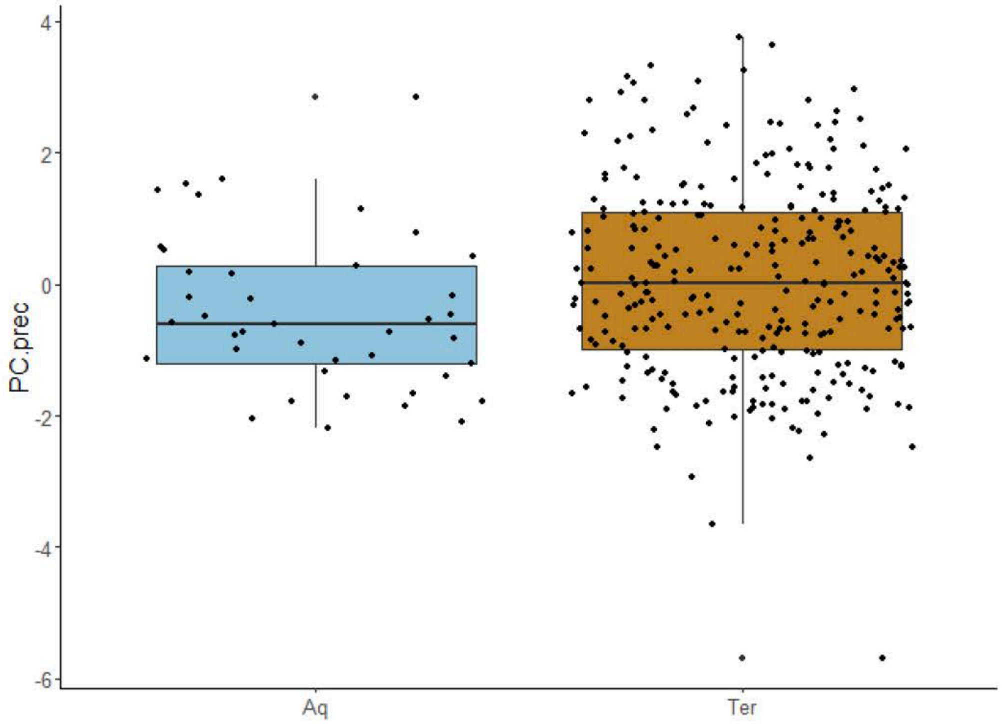


Figure 1d



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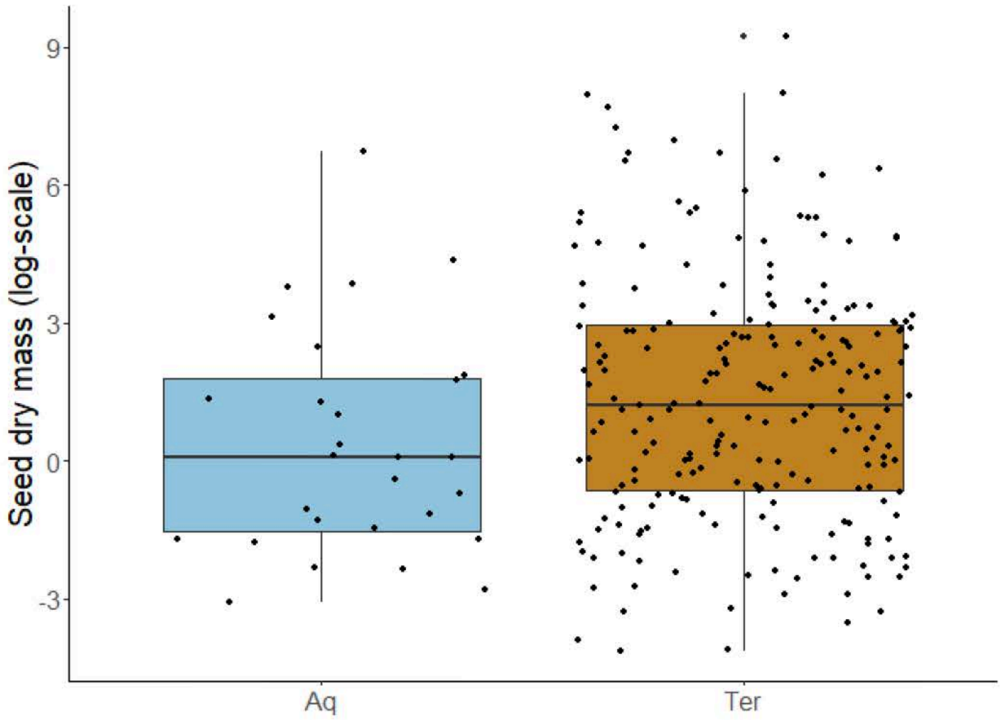
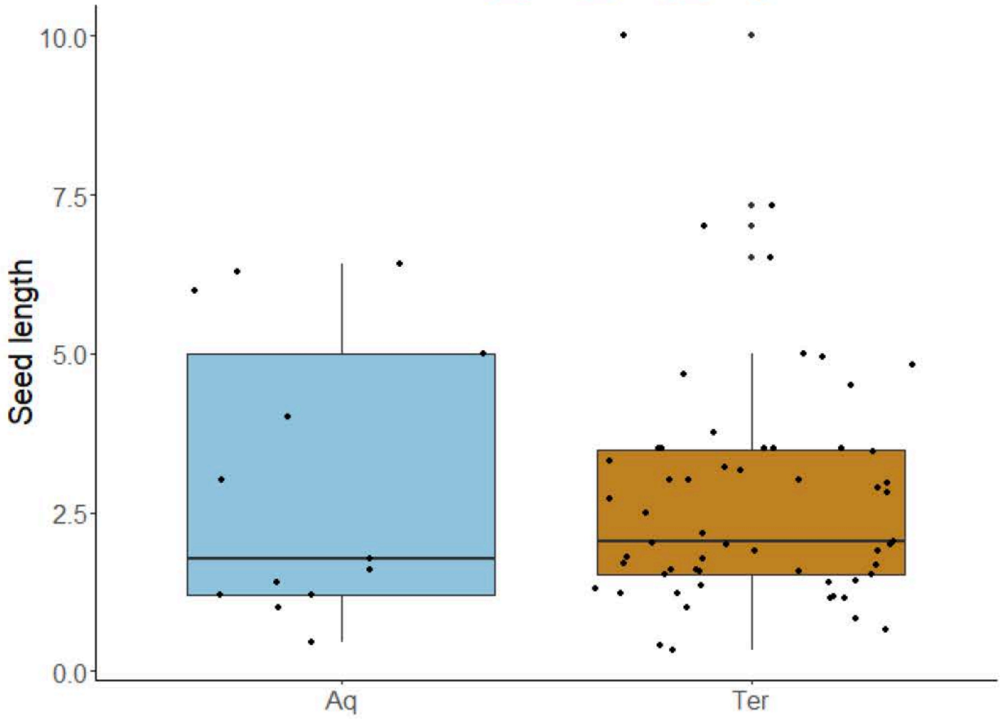


Figure 1f



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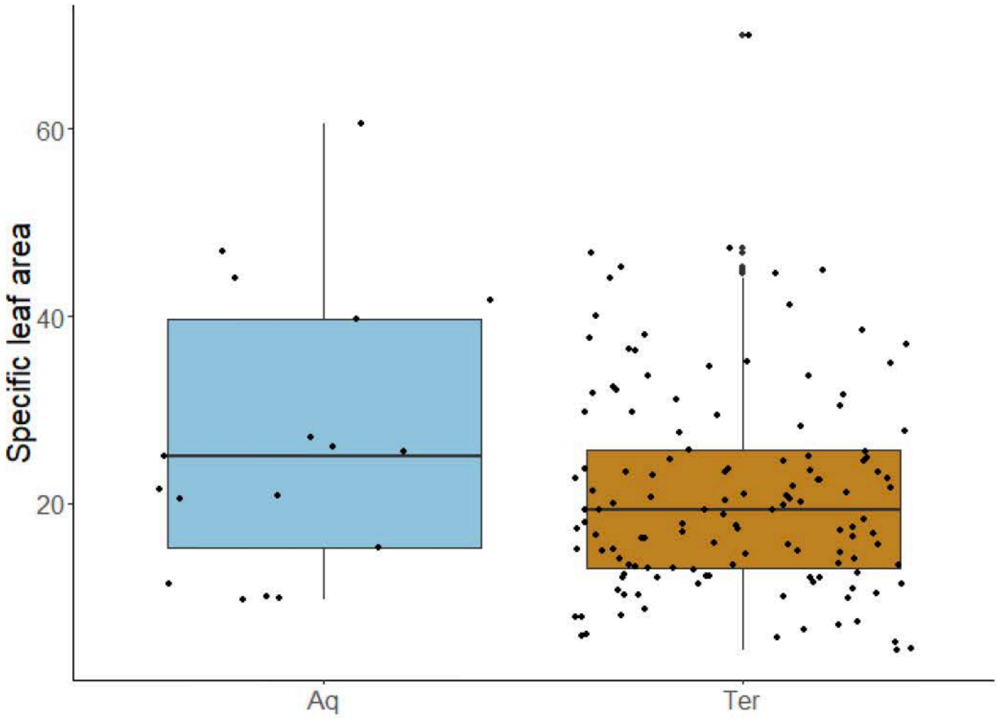
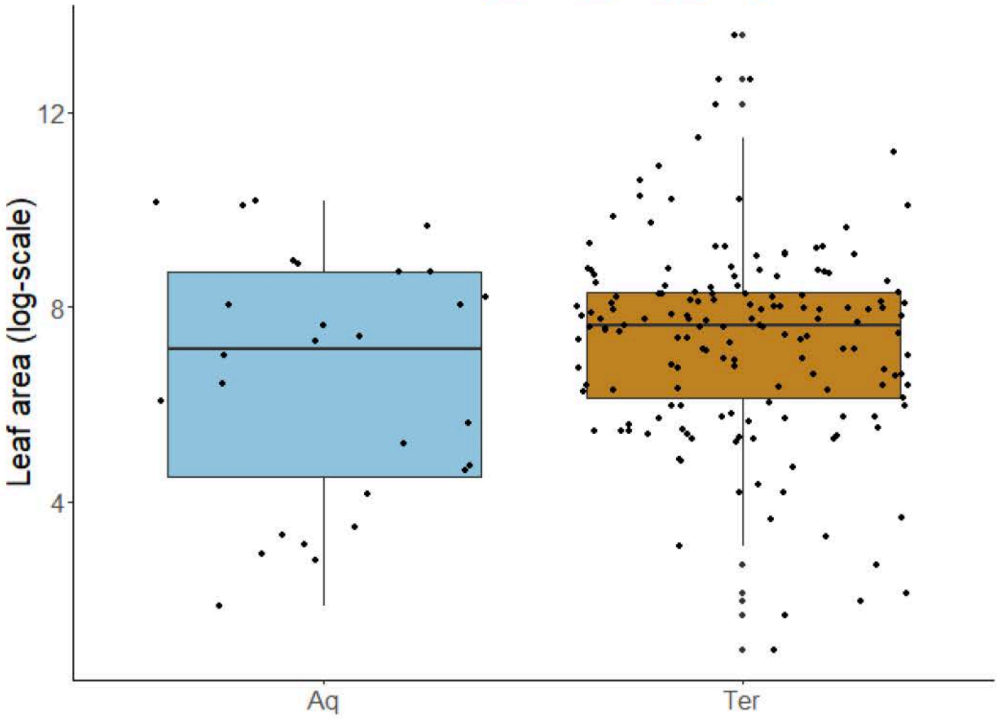


Figure 1h



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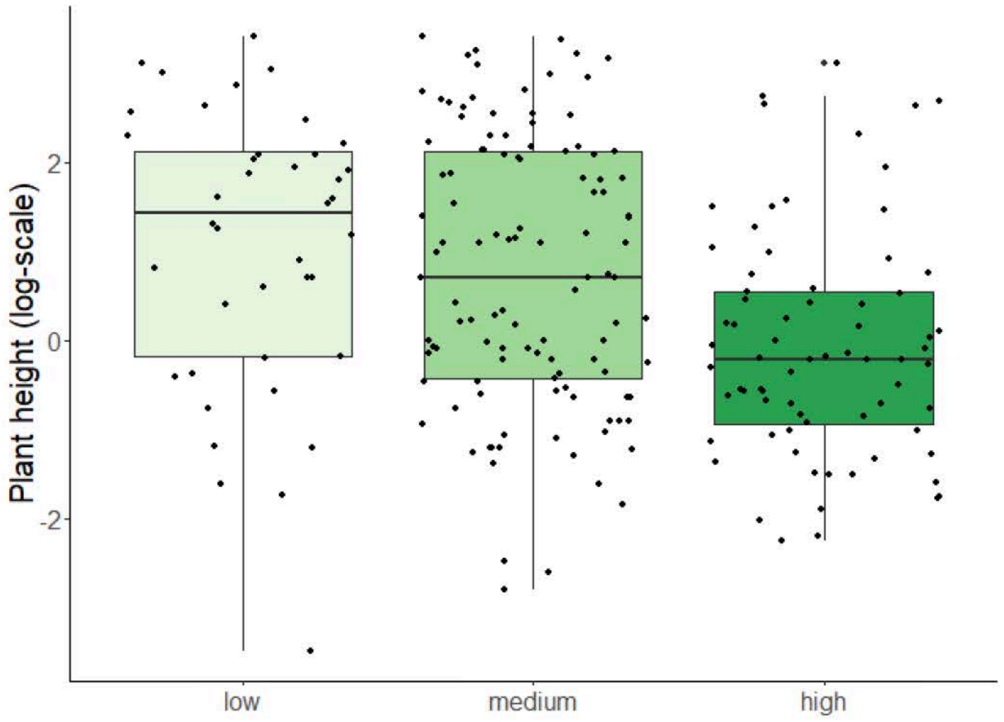

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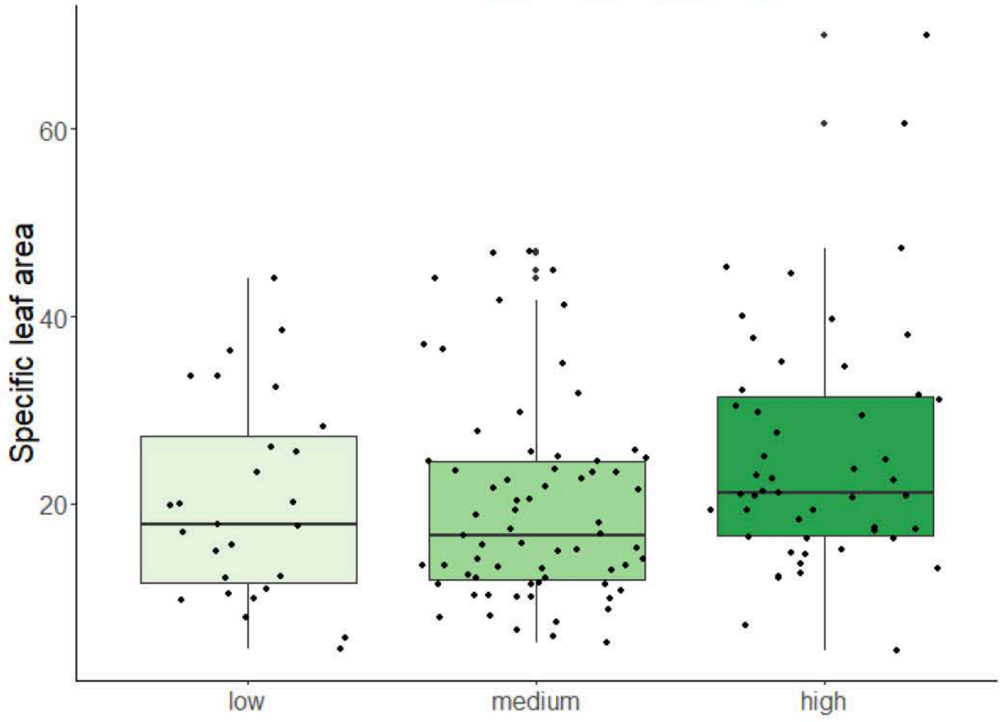

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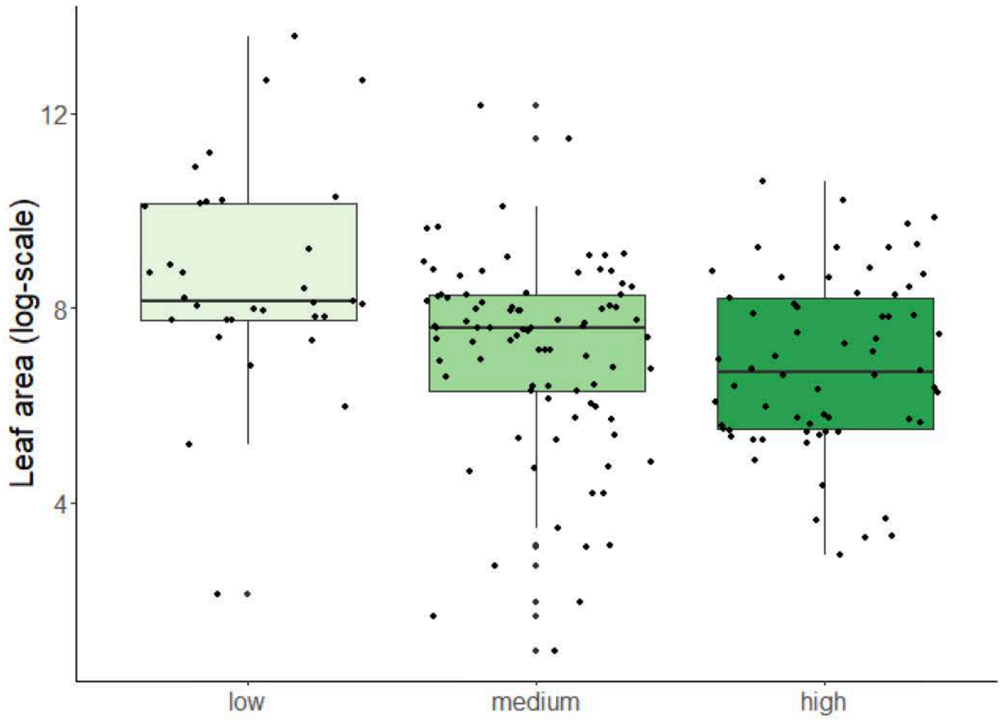

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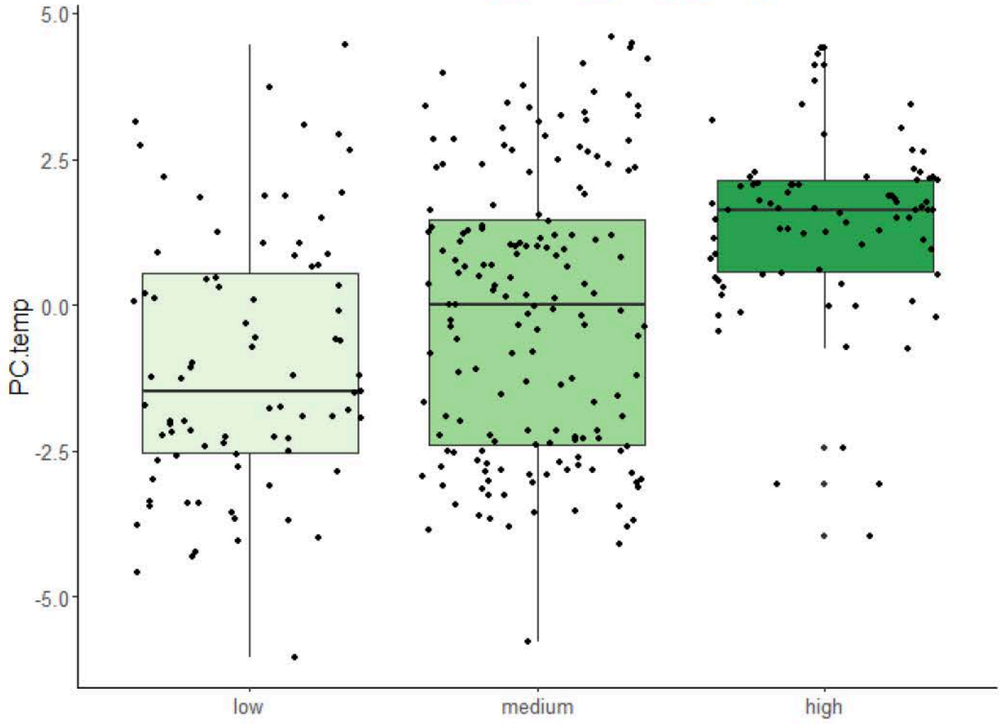

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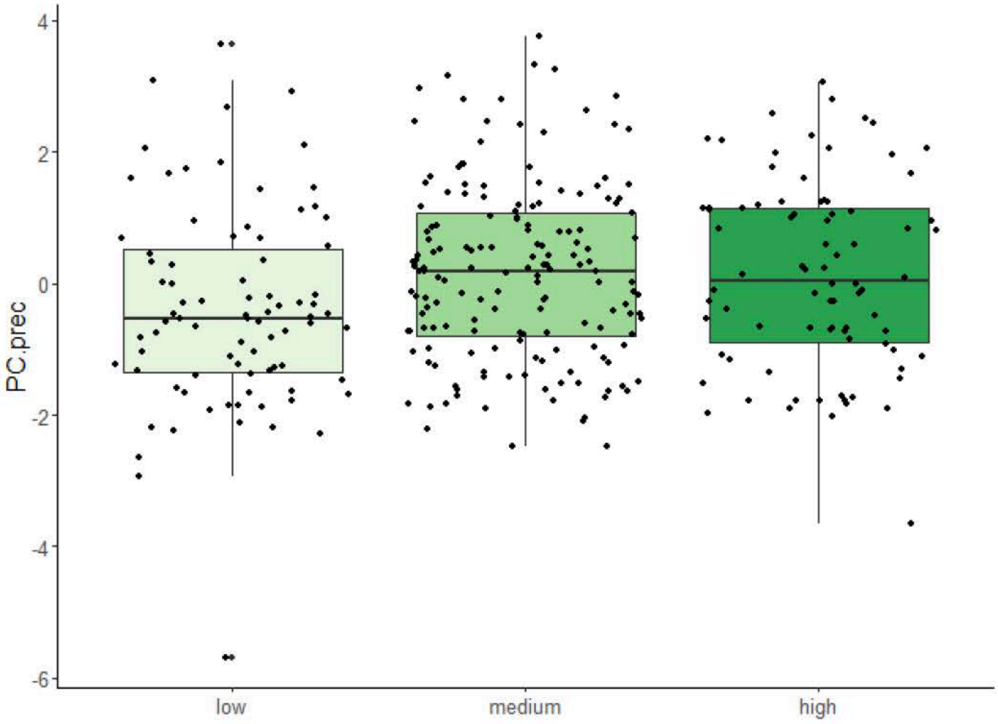

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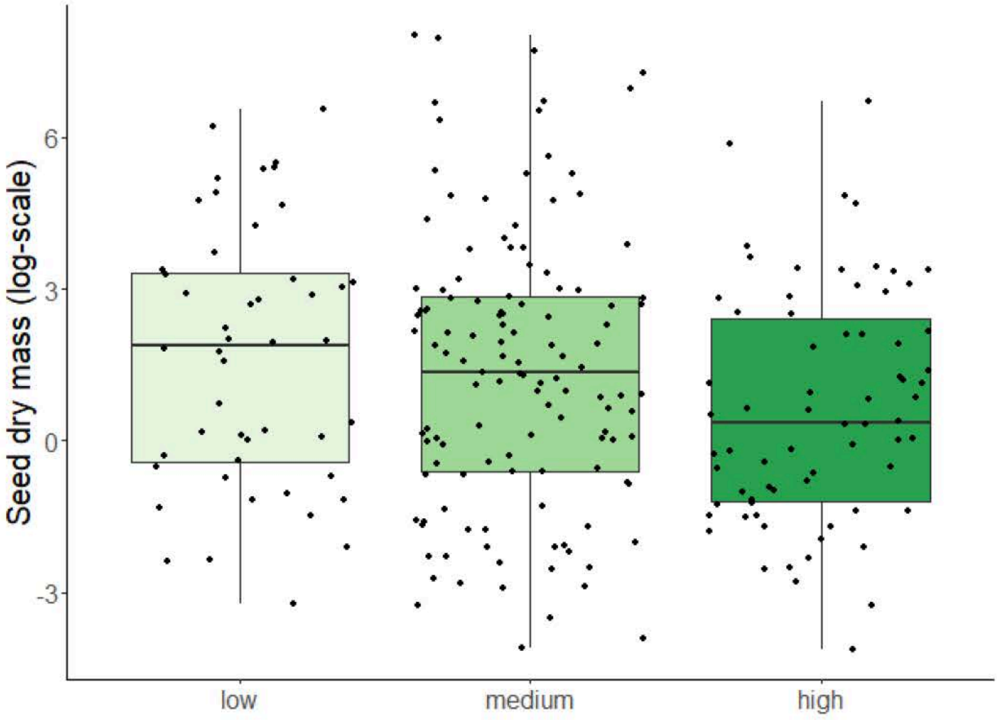

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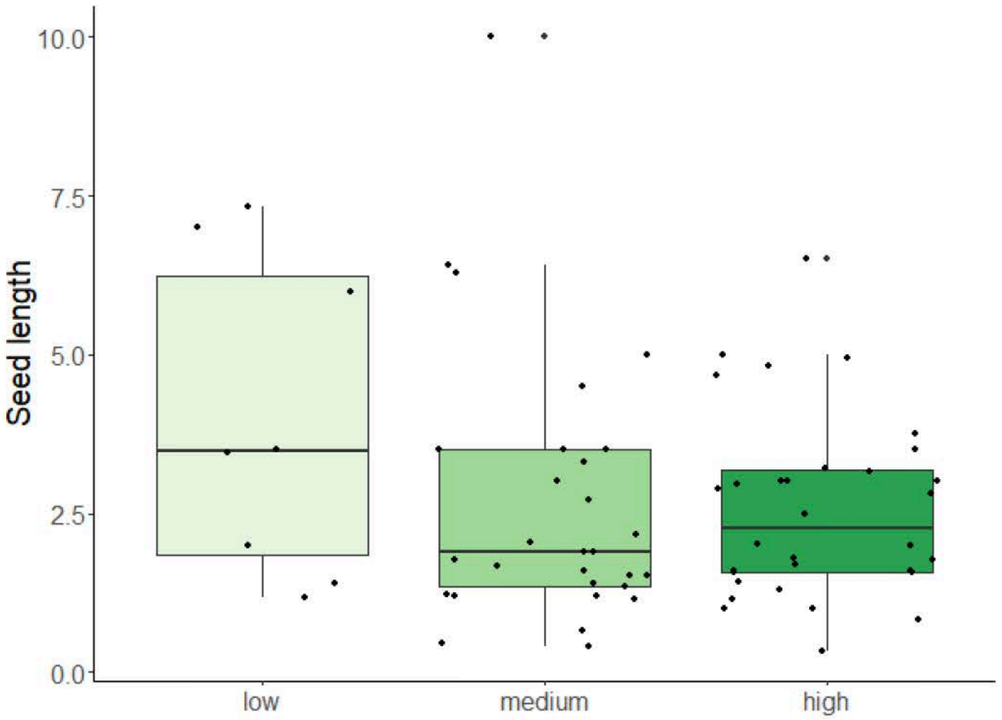

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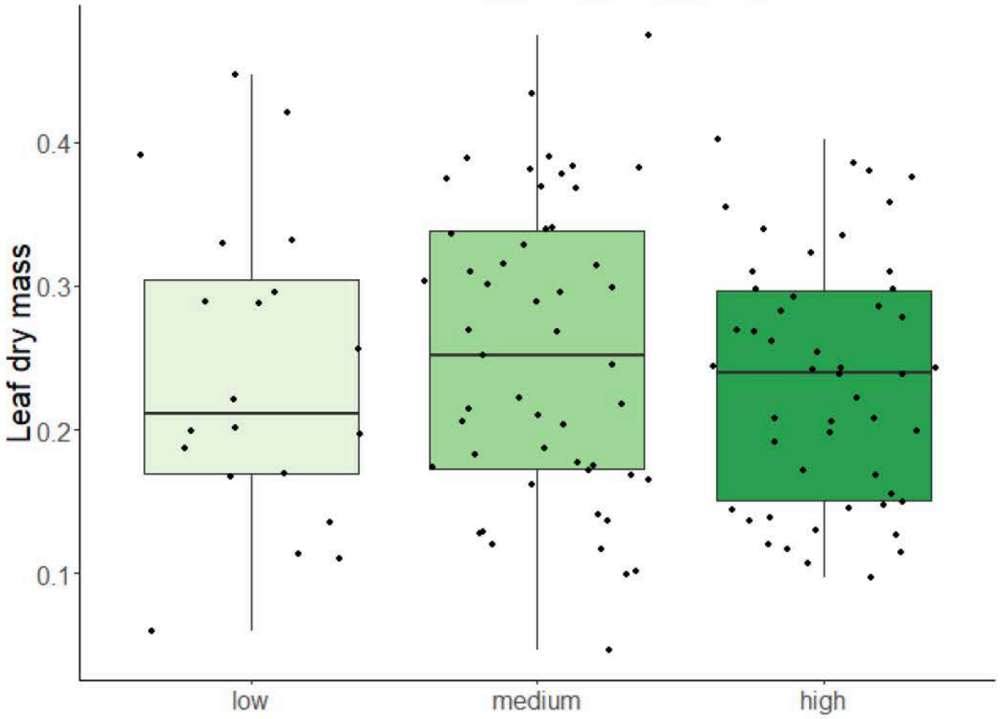
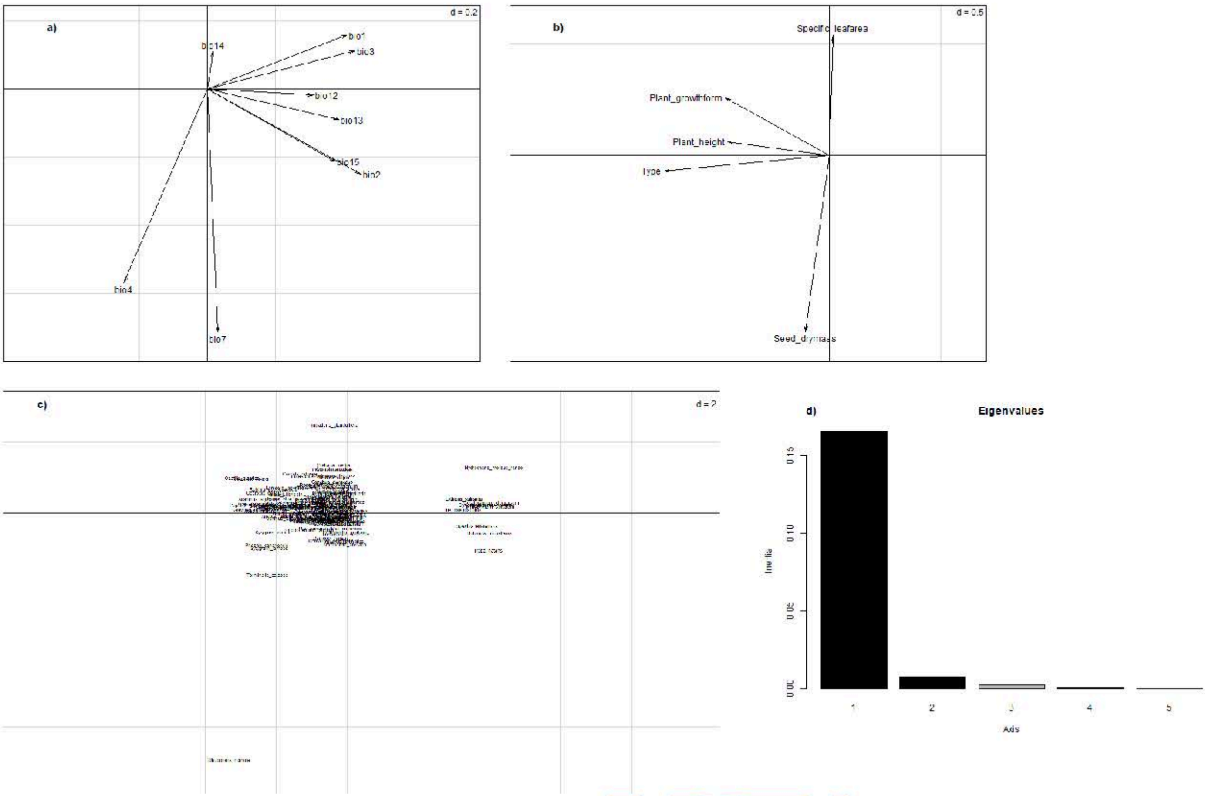


Figure 3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bio1
bio3
bio12
bio13
bio15
bio2
bio4
bio7
b)
d = 0.5
Specific_leafarea
Plant_growthform
Plant_height
Type
Seed_drymass
c)
d = 2
d)
Eigenvalues
Inertia
0.15
0.10
0.05
0.00
1
2
3
4
5
Axis