Universidade do Estado do Rio de Janeiro
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Ilaíne Silveira Matos

Estabilidade de comunidades vegetais diante das mudanças climáticas: o efeito da diversidade funcional e das fontes alternativas de água na resposta das vegetações campestres à seca

Rio de Janeiro
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Tese apresentada, como requisito parcial para obtenção do título de Doutora, ao Programa de Pós-Graduação em Ecologia e Evolução da Universidade do Estado do Rio de Janeiro. Área de concentração: Ecologia de Comunidades e Ecossistemas.

Orientador: Prof. Dr. Bruno Henrique Pimentel Rosado

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Ilaíne Silveira Matos

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Rio de Janeiro
2019

DEDICATÓRIA

Dedico este trabalho a todos os professores da UERJ, que no ano de 2017, enfrentaram uma das piores crises desta universidade. Sem, contudo, desistir da luta por uma educação pública, gratuita e de qualidade.

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Depois de uma longa jornada de quatro anos eu descobri que para ser doutora em Ecologia é preciso aprender muito mais do que ser ecóloga. É preciso ser um pouco de fotógrafa, motorista, cozinheira, decoradora, pintora de aquarelas, maratonista, programadora, mecânica, professora, anatomista, padeira, tradutora, escritora, trilheira, organizadora de festas surpresas e até depiladora de folhas. Obviamente eu não aprendi a ser e a fazer tudo isso sozinha. Pelo contrário, tive a imensa sorte de ter ao meu redor pessoas sempre dispostas a me ajudar. As quais agradeço agora.

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RESUMO

MATOS, I. S. *Estabilidade de comunidades vegetais diante das mudanças climáticas:* o efeito da diversidade funcional e das fontes alternativas de água na resposta das vegetações campestres à seca. 2019. 216f. Tese. (Doutorado em Ecologia e Evolução) - Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro 2019.

Uma questão central na Ecologia é desvendar fatores que expliquem a variação na estabilidade entre sistemas biológicos. Considerando o aumento na intensidade, duração e frequência dos eventos de seca, o objetivo geral deste estudo foi investigar os efeitos de dois fatores: diversidade funcional (diversidade no modo como as espécies respondem aos distúrbios e/ou estresses e afetam o funcionamento do sistema) e o uso de fontes alternativas de água (neblina), na resposta da vegetação à seca. Esses efeitos foram avaliados particularmente sobre a estabilidade das vegetações campestres. Já que elas recobrem larga porção da superfície terrestre e têm sua produtividade predominantemente controlada pela precipitação. Primeiramente, uma meta-análise de experimentos de manipulação de chuva foi realizada a fim de avaliar a estabilidade geral na produção de biomassa aérea; e de quantificar a importância relativa das características da seca e das condições climáticas para explicar a variação de estabilidade entre 101diferentes vegetações. De modo geral, esses sistemas se mostraram resilientes, i.e. se mantiveram inalterados após a seca; porém diferiram na sua capacidade de resistir, i.e. se manter inalterado durante a seca, e de se recuperar, i.e. compensar os danos sofridos durante a seca, resultando numa relação negativa entre essas duas últimas propriedades. Tanto as características das secas, como as condições climáticas, não foram capazes de explicar essas diferenças. Logo, outros fatores como propriedades do solo e/ou características intrínsecas da vegetação, como diferenças na diversidade funcional, podem ser mais importantes para determinar a variação na estabilidade na resposta à seca. Em seguida, o efeito da diversidade funcional foi avaliado utilizando-se os Campos de Altitude como sistema-modelo. Através da integração de estratégias eco-fisiológicas e de índices de originalidade funcional foi possível predizer a estabilidade das comunidades vegetais sob diferentes cenários de extinção de espécies. Devido à presença de um grande número de espécies resistentes à seca, os Campos de Altitude se mostraram estáveis na maioria dos cenários avaliados.Contudo, instabilidade foi observada nos cenários em que houve a perda de espécies não-resistentes, as quais se baseiam na absorção de neblina para lidar com a seca. Este pequeno grupo se mostrou como um dos mais sensíveis a seca, devendo, portanto, receber prioridade de conservação. Finalmente, foi investigado o porquê algumas espécies se beneficiam mais da neblina do que outras, e quais as implicações ecológicas dessa variação num cenário de mudanças climáticas. Foi demonstrado que características foliares e estratégias ecológicas das espécies podem explicar essa variação interespecífica, com espécies ruderais exibindo maior absorção do que as espécies tolerantes ao estresse. Conclui-se que apesar das vegetações campestres serem resilientes à seca em termos de biomassa, elas podem ser instáveis quanto à diversidade funcional. Num futuro com mais secas e menos neblina, as espécies resistentes poderão suplantar as não-resistentes, resultando na perda de diversidade. Sugere-se que futuros experimentos submetam as vegetações a secas mais extremas e monitorem o desempenho durante o período pós-seca a fim de testar essas previsões e de continuar avançando no conhecimento dos mecanismos subjacentes à estabilidade.

Palavras-chave: Absorção foliar de água. Campos de altitude. Originalidade funcional. Recuperação. Redundância funcional. Resiliência. Resistência.

ABSTRACT

MATOS, I. S. *Plant community stability under climate change*: the effect of functional diversity and alternative sources of water on grasslands response to drought. 2019. 216f. Tese (Doutorado em Ecologia e Evolução) - Instituto de Biologia Roberto Alcântara Gomes, Universidade do Estado do Rio de Janeiro, Rio de Janeiro 2019.

Unveiling the factors underlying differential stability across biological systems remains one of the most fundamental questions in Ecology. Considering the worldwide increase in drought intensity, duration and frequency, the main goal of this study was to investigate the role of two factors, functional diversity (diversity on species response to disturbances and/or stresses and on their effects on the ecosystem functioning) and use of alternative water sources (fog) on plants response to drought. Since grasslands cover a large proportion of the terrestrial land surface and their productivity is controlled by precipitation, those factors were evaluated, particularly, on grassland stability. Firstly, a meta-analysis of manipulation rainfall experiments performed on 101 grasslands locations distributed worldwide was conducted to evaluate the general stability on biomass production; and to quantify the relative importance of drought features and prevailing conditions in explaining stability variation. On average, grasslands were resilient to drought, they kept biomass unchanged after drought; but significantly differed on their ability to resist, to keep biomass unchanged during drought, and to recover, to compensate damages incurred during drought, leading to a negative relationship between the last two properties. Those differences were not explained by either experimental drought features, nor by prevailing conditions. This suggests that soil and/or intrinsic biotic features, such as the degree of functional diversity, could be more important to determine differential stability across grasslands. A new conceptual framework, integrating eco-physiological strategies and functional originality indices was then proposed, in order to assess the role of functional diversity and to predict community stability under distinct scenarios of species loss. The framework was applied, using the Campos de Altitude, a Brazilian tropical mountain grassland vegetation, as a model system. The general stability of Campos de Altitude would be ensured under most of the evaluated scenarios, due to the presence of a large number of resistant species. However, instability was observed for scenarios where a small group of non-resistant species, which rely on foliar water uptake to deal with drought were lost (i.e. absorption of fog through leaves, FWU). Those species were one of the group most sensitive to drought, and thus conservation priorities should be assigned on them. Finally, the interspecific variation in FWU was investigated, and the ecological implications of this variation under climate change scenario was assessed. It was shown that species foliar traits and ecological strategies could explain this variation, with ruderal species showing greater FWU than stress-tolerant species. In conclusion, although grasslands were resilient to drought in terms of above-ground biomass, their functional diversity migh be unstable. In a future with more droughts and less fog, resistant species could outperform non-resistant ones, leading to a functional homogenisation. Future experiments should subject vegetation to more extreme droughts, in order to test those predictions and to develop a better understanding about the mechanisms underlying differential stability across biological systems.

Keywords: Campos de altitude. Foliar water uptake. Functional originality. Functional redundancy. Recovery. Resilience. Resistance.

LISTA DE ABREVIATURAS E SIGLAS

%PPT –	Porcentagem de precipitação interceptada nas parcelas de seca
AB –	Abaxial
AD –	Adaxial
AICc –	Variante de segunda ordem do critério de informação de Akaike
ANCOVA –	Análise de covariância
ANOVA –	Análise de variância
Asl	Acima do nível do mar
BC_n –	Biomassa amostrada nas parcelas controle durante o período de seca
BC_{pd} –	Biomassa amostrada nas parcelas controle durante o período de pós-seca
BD_n –	Biomassa amostrada nas parcelas de seca durante o período de seca
BD_{pd} –	Biomassa amostrada nas parcelas de seca durante o período de pós-seca
BHPMF –	Fatoração da matriz probabilística hierárquica bayesiana
Bi –	Biomassa aérea seca inicial
Br –	Biomassa aérea seca após rebrota
CAPES –	Coordenação de Aperfeiçoamento de Pessoal de Nível Superior
CI –	Intervalo de confiança
CR –	Competidora-ruderal
CS –	Competidora-tolerante ao estresse
CSR –	Competitividade; tolerância ao estresse; ruderalismo
DIF –	Diferença absoluta na precipitação entre as parcelas controle e de seca
DIS –	Distintividade
FAPERJ –	Fundação de amparo à pesquisa do estado do Rio de Janeiro
FD –	Diversidade funcional
FDR –	Taxa de descoberta falsa
FG –	Grupo funcional
Fgc –	Fração média da superfície foliar alocada para células guarda
FO –	Originalidade funcional
Freq –	Frequência da espécie na área de estudo
Fsp –	Fração média da superfície foliar alocada para poros estomáticos
FWU –	Absorção foliar de água

FWU_{flux} –	Absorção foliar de água – fluxo
FWU_{lwc} –	Absorção foliar de água – conteúdo hídrico foliar
FWU_{lwr} –	Absorção foliar de água – retorno
g_{smd} –	Condutância estomática máxima ao meio dia
g_{smean} –	Condutância estomática média
INP –	Parque Nacional do Itatiaia
LA –	Área foliar
LDMC –	Conteúdo de massa seca foliar
LES –	Espectro foliar econômico
LEV –	Laboratório de ecologia vegetal
Lth –	Espessura foliar
LWH –	Repelência foliar de água
LWR –	Retenção foliar de água
MAP –	Precipitação média anual
MAT –	Temperatura média annual
PC1 –	Primeiro componente principal
PC2 –	Segundo componente principal
PC3 –	Terceirocomponente principal
PCA –	Análise de componentes principais
PNI –	Parque Nacional do Itatiaia
PNT –	Parque Nacional Floresta da Tijuca
$PPTC_{n}$ –	Precipitação recebida pelas parcelas controle durante o período de seca
$PPTC_{pd}$ –	Precipitação recebida pelas parcelas controle durante o período de pós-seca
$PPTD_{n}$ –	Precipitação recebida pelas parcelas de seca durante o período de seca
$PPTD_{pd}$ –	Precipitação recebida pelas parcelasde seca durante o período de pós-seca
RA –	Capacidade de rebrota
RC –	Recuperação
RRS –	Resiliêcia relativa
RS –	Resiliência
RT –	Resistência
sd –	Desvio padrão
SD –	Densidade estomática
SES –	Tamanho de efeito padronizado

SISBIO –	Sistema de autorização e informação em biodiversidade
SLA –	Área foliar específica
SPEI –	Índice padronizado de precipitação evapotranspiração
SS –	Tamanho da semente
SSD –	Densidade específica do caule
SPAC –	Contínuo solo-planta-atmosfera
SUC –	Suculência foliar
Trich –	Tricomas foliares
UERJ –	Universidade do Estado do Rio de Janeiro
UFRJ –	Universidade Federal do Rio de Janeiro
UFRRJ –	Universidade Federal Rural do Rio de Janeiro
UNI –	Singularidade
VD –	Densidade de venação
VPD –	Déficit de pressão de vapor
Δslope –	Comportamento iso-anisohídrico
$\Psi_{gs50\%}$–	Potencial hídrico foliar quando a condutância estomática é reduzida para 50 % do seu máximo
Ψ_{leaf} –	Potencial hídrico foliar
Ψ_{md} –	Potencial hídrico foliar ao meio dia
Ψ_{mean} –	Potencial hídrico foliar médio sazonal
Ψ_{min} –	Potencial hídrico foliar mínimo sazonal
Ψ_{pd} –	Potencial hídrico foliar de madrugada
Ψ_{tlp} –	Potencial hídrico foliar no ponto de perda de turgor

SUMÁRIO

INTRODUÇÃO GERAL

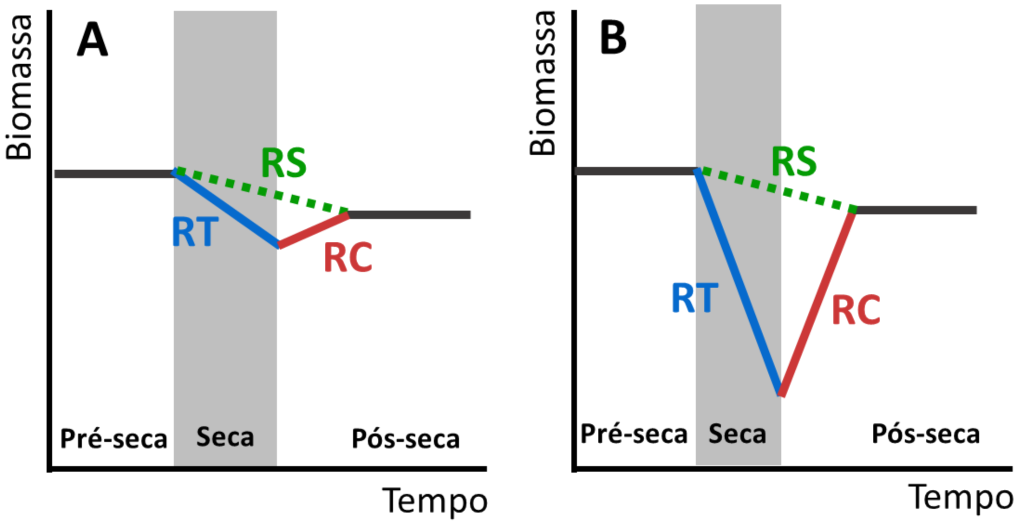
As atividades humanas têm provocado o progressivo aumento nas concentrações atmosféricas de gases do efeito estufa, levando ao aquecimento da superfície terrestre e a intensificação do ciclo hidrológico a nível global (Min et al. 2011). Como consequência, se observam alterações na quantidade, sazonalidade, variabilidade e extremidade do regime de chuvas, bem como mudanças na contribuição relativa das diferentes fontes de água, como chuva, neve, neblina e orvalho (Huntington 2006, IPCC 2013). Prevê-se que os eventos de seca se tornarão mais intensos e duradouros, e até o final deste século, a sua frequência deverá triplicar, ao mesmo tempo em que a proporção de superfície terrestre sujeita a seca passará de 1 para 30% (Burke et al. 2006, Sheffield e Wood 2007).

Para alguns tipos de vegetação a água já constitui um recurso limitante, e esta limitação poderá, então, se agravar em decorrência dessas mudanças no regime de precipitação (Chaves e Oliveira 2004). Estudos observacionais e experimentais investigando os efeitos de tais mudanças sobre as comunidades vegetais têm encontrado resultados divergentes (Stuart-Haëntjenset al. 2018, Wilcox et al. 2017, Wu et al. 2011). Em alguns casos, secas extremas (i.e. episódios climáticos estatisticamente raros, Smith 2011) culminam em respostas biológicas extremas (i.e. alterações na estrutura e/ou na função que excedem o padrão normal de variabilidade e demandam longos períodos de recuperação, ou são irrecuperáveis, Smith 2011), provocando aumento na mortalidade, redução no crescimento e mudanças na fenologia, na distribuição espacial e nas interações entre os organismos (Carnicer et al. 2011, Parmesan e Hanley 2015). Em outros casos, porém, pouco ou nenhum efeito foi observado (Lloret et al. 2012, Smith 2011). Por isso, uma questão central na Ecologia tem sido não somente identificar quais sistemas biológicos (i.e. indivíduos, populações, comunidades, biomas) são menos estáveis em respota às mudanças climáticas. Mas, principalmente, entender quais os mecanismos responsáveis por determinar esses distintos graus de estabilidade (Sutherland et al. 2013, Williams et al. 2008).

Estabilidade, contudo, é um dos termos mais nebulosos na Ecologia, com mais de 163 diferentes definições catalogadas (Grimm e Wissel 1997) e inúmeras métricas indistintamente utilizadas para acessá-la (Ingrisch e Bahn 2018). As primeiras tentativas de determinar a estabilidade de sistemas biológicos se basearam no conceito de resiliência; definida, ou como o tempo necessário para um sistema retornar ao seu estado de equilíbrio após sofrer um distúrbio (‘*engineering resilience*’ Pimm 1984); ou como a quantidade de distúrbio que um sistema pode absorver antes de mudar para um novo estado de equilíbrio ('*ecological resilience*' Holling 1973). Enquanto a primeira definição pressupõe a existência de apenas um único estado de equilíbrio e considera a estabilidade como a capacidade do sistema manter a eficiência de suas funções, a segunda reconhece a possibilidade de haver dois ou mais estados alternativos e enfatiza a manutenção da existência das funções do sistema (Gunderson e Holling 2002). Recentes tentativas de padronizar tanto as definições como os índices de estabilidade, identificam a estabilidade como um conceito complexo e multidimensional (Hodgson et al. 2015, Ingrisch e Bahn 2018, Nimmoet al. 2015, Standish et al. 2014), e que deve envolver pelo menos três propriedades distintas (Figura 1): (1) resistência (RT), definida como a capacidade do sistema se manter inalterado *durante* o distúrbio e/ou estresse; (2) recuperação (RC), capacidade do sistema compensar as mudanças ocorridas durante o distúrbio e/ou estresse; e (3) resiliência (RS), capacidade do sistema se manter inalterado *após* o distúrbio e/ou estresse (Lloret et al. 2011, Van Ruijven e Berendse 2010). Partindo dessa abordagem multidimensional, diferentes sistemas podem atingir um mesmo grau de estabilidade através de diferentes trajetórias; bem como podem existir demandas conflitantes (i.e.*'trade-offs'*) entre essas três propriedades (Donohue et al. 2013, Oliver et al. 2015). Por exemplo, considerando duas comunidades vegetais sujeitas a um evento de seca (Figura 1); uma delas pode se mostrar resiliente, em termos de produção de biomassa, porque sua biomassa não se altera muito durante a seca (i.e. alta resistência, baixa recuperação, Figura 1A); enquanto que na outra há uma maior perda de biomassa durante a seca, mas esta é, em grande parte, recuperada após o término da seca (i.e. baixa resistência, alta recuperação, Figura 1B).

Além de multidimensional, a estabilidade é também um conceito quantitativo e processo-específico; e não uma propriedade genérica e qualitativa do sistema. Portanto, em qualquer situação, o primeiro passo para se determinar a estabilidade de um sistema é especificar claramente qual o distúrbio e/ou estresse e qual a variável ecológica de interesse (Carpenter et al. 2011). Considerando o exemplo acima, tem-se a seca como fator de distúrbio e/ou estresse e a biomassa como variável ecológica de interesse. Conforme exposto, ambos os sistemas apresentam alta resiliência em termos de biomassa. Porém, se a resiliência for acessada em termos de composição de espécies, os resultados podem ser diferentes. Na segunda comunidade, por exemplo, a recuperação da biomassa após o evento de seca poderia ter ocorrido justamente através de mudanças na composição e abundância das espécies; com a perda inicial de espécies sensíveis a seca e sua posterior substituição por espécies mais resistentes e/ou resilientes. Assim, a não-resiliência na composição de espécies pode ser precisamente o mecanismo que assegura a resiliência da biomassa da comunidade (Hooper et al. 2005, Oliver et al. 2015).

Figura 1 - As três propriedades da estabilidade: resistência (RT), recuperação (RC) e resiliência (RS).



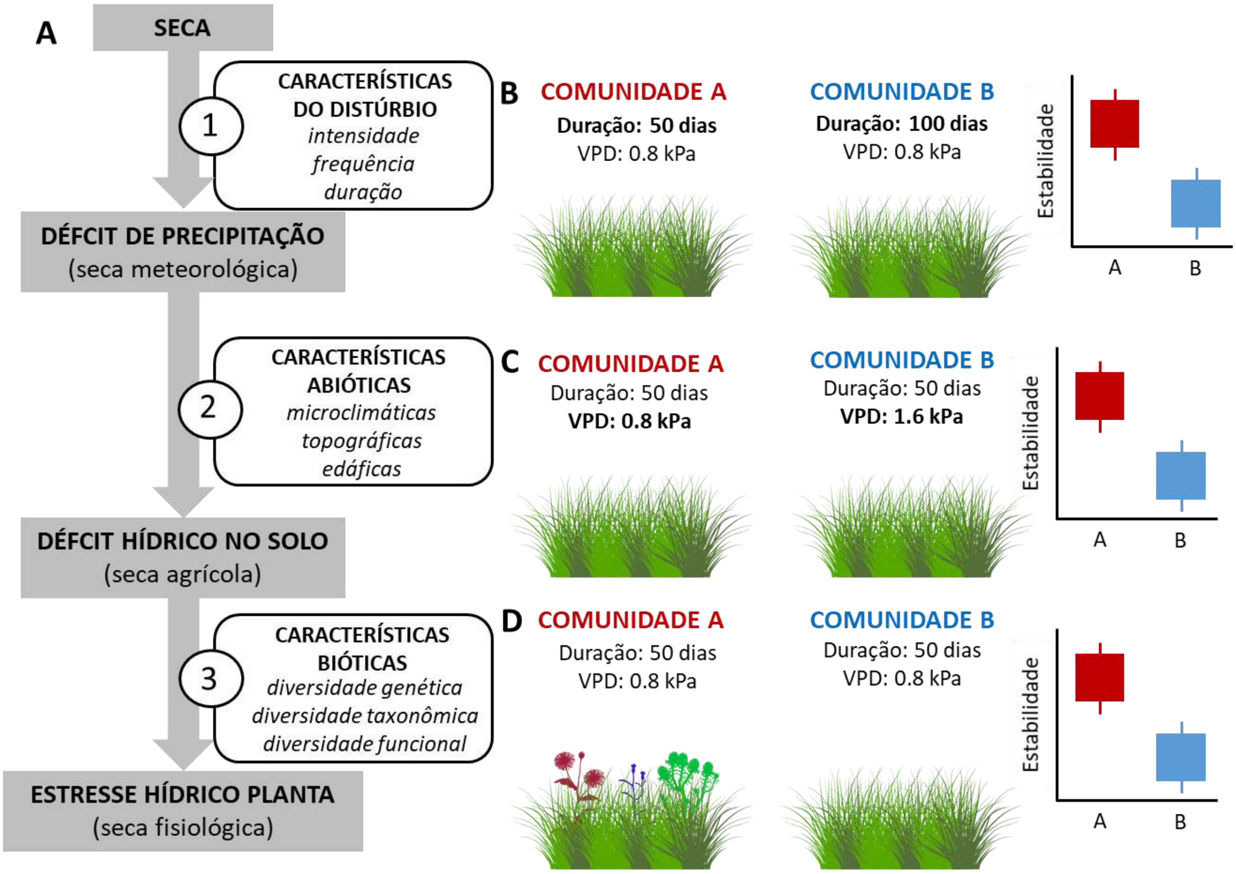
Legenda: considerando a seca como fator de distúrbio e/ou estresse e a biomassa vegetal como variável ecológica de interesse, a estabilidade pode ser acessada como:resistência (RT), capacidade do sistema manter a biomassa inalterada durante a seca; recuperação (RC), capacidade do sistema produzir nova biomassa após a seca; e resiliência (RS), capacidade do sistema manter a biomassa inalterada após a seca; ou seja, o sistema é resiliente se a biomassa no pós-seca é similar aos valores de biomassa antes da seca (pré-seca). (A) A comunidade apresenta alta resiliência à seca, em termos de produção de biomassa, porque sua biomassa não se altera muito durante a seca (i.e. alta RT, baixa RC); (B) A comunidade apresenta alta resiliência à seca porque apesar de perder biomassa durante a seca, ela é capaz de recuperar boa parte da biomassa perdida após o término da seca (i.e. baixa RT, alta RC).

Fonte: Adaptado de Lloret et al. 2011.

Após a seleção das propriedades da estabilidade (RT, RC, RS); do fator de distúrbio e/ou estresse (seca) e da(s) variável(is) ecológicas de interesse (biomassa, composição), torna-se possível comparar a estabilidade entre diferentes comunidades vegetais; e, consequentemente, desvendar os mecanismos que explicam a sua variação. Três principais conjuntos de fatores têm sido apontados como responsáveis pela variação na estabilidade em resposta à seca (Anderegget al. 2013, Mitchell et al. 2016, Smith et al. 2009): (1) características do distúrbio e/ou do fator de estresse, como intensidade, frequência, duração e escala espaço-temporal do evento de seca em termos de precipitação (i.e. seca metereológica);

(2) características abióticas do sistema, como fatores climáticos (temperatura, déficit de pressão de vapor - VPD, vento, radiação), topográficos (inclinação) e edáficos (tipo do solo, textura, profundidade) que influenciam a demanda evaporativa do ar e a infiltração de água no solo e, consequentemente, medeiam o modo como o déficit de precipitação (i.e. seca metereológica) se traduz num déficit de água no solo (i.e. seca agrícola);e (3) características bióticas do sistema, como o seu nível de diversidade (genética, taxonômica e funcional), que vão determinar como o déficit de água no solo se traduz (ou não) num estresse hídrico para as plantas (i.e. seca fisiológica: discrepância entre o suprimento e a demanda de água para a planta que resulta em limitações hidráulicas ao seu desenvolvimento e sobrevivência, Dai 2010) (Figura 2A). A Figura 2B-D exemplifica os efeitos desses três conjuntos de fatores, comparando a estabilidade, em termos de biomassa, entre duas comunidades hipotéticas (A e B) em resposta a um evento de seca. No primeiro caso (Figura 2B), as duas comunidades são idênticas nas características bióticas (e.g. diversidade funcional) e abióticas (e.g. VPD). Porém, a comunidade B exibe menor estabilidade simplesmente por ter sido submetida a uma seca de maior duração. No segundo caso (Figura 2C), as comunidades apenas diferem em relação a característica abiótica. O maior VPD na comunidade B resulta em uma maior demanda evaporativa do ar, menor disponibilidade de água no solo, menor produção de biomassa durante a seca, e consequentemente, menor estabilidade. Por fim, no terceiro caso (Figura 2D), as comunidades são submetidas a secas semelhantes e tem mesmo VPD. Mas, diferem quanto a diversidade funcional. Assim, a estabilidade da comunidade B é novamente menor, pois ela é dominada por espécies sensíveis a seca (menor diversidade funcional); enquanto a comunidade A é constituída por uma diversidade de espécies que exibem diferentes estratégias para lidarem com o déficit hídrico (maior diversidade funcional). Embora vários estudos tenham avaliado os efeitos individuais desses diferentes fatores, ainda pouco se sabe sobre a importância relativa de cada um deles, e de suas possíveis interações, para explicar a variação na estabilidade entre as comunidades vegetais.

Figura 2 - Diagrama conceitual exemplificandoos efeitos potenciais de três conjuntos de fatores (características do distúrbio e/ ou estresse, características abióticas e características bióticas) sobre a estabilidade, em termos de biomassa, entre duas comunidades vegetais hipotéticas (A e B) em resposta a um evento de seca.



Legenda: (A) -a estabilidade das comunidades vegetais em resposta a seca depende de pelo menos três conjuntos de fatores: das características do distúrbio e/ou estresse, como as características de um evento de seca (seca metereológica: déficit de precipitação); das características abióticas do sistema, que medeiam como o déficit de precipitação se traduz num déficit de água no solo (seca agrícola); e das características bióticas do sistema, que medeiam como o déficit de água no solo se traduz num estresse hídrico para as plantas (seca fisiológica); (B) -comunidades A e B exibem características abióticas (VPD – déficit de pressão de vapor) e bióticas (diversidade funcional) idênticas; mas, a comunidade B exibe menor estabilidade por ter sido submetida a uma seca de maior duração (100 dias), do que a comunidade A (50 dias); (C) -comunidades A e B foram submetidas a secas de mesma duração e tem mesma diversidade funcional; mas, a comunidade B exibe menor estabilidade por ter sido submetida a uma maior demanda evaporativa do ar (maior VPD) durante o evento de seca; (D) -comunidades A e B foram submetidas a secas idênticas e tem mesmas características abióticas; mas, a comunidade B exibe menor estabilidade por ser dominada por espécies sensíveis a seca (menor diversidade funcional); enquanto que a comunidade A é constituída por uma diversidade de espécies que exibem diferentes estratégias para lidarem com o déficit hídrico (maior diversidade funcional).

Fonte: O autor, 2019.

O efeito da diversidade funcional

Há uma vasta literatura sugerindo que comunidades com uma maior diversidade de espécies seriam mais estáveis em resposta a variados tipos de distúrbios, sendo essa relação positiva explicada por duas classes gerais de mecanismos (Loreau e Hector 2001): efeitos de complementariedade (*'complementarity effects'*) e efeitos de seleção (*'selection effects'*) (Figura 3).

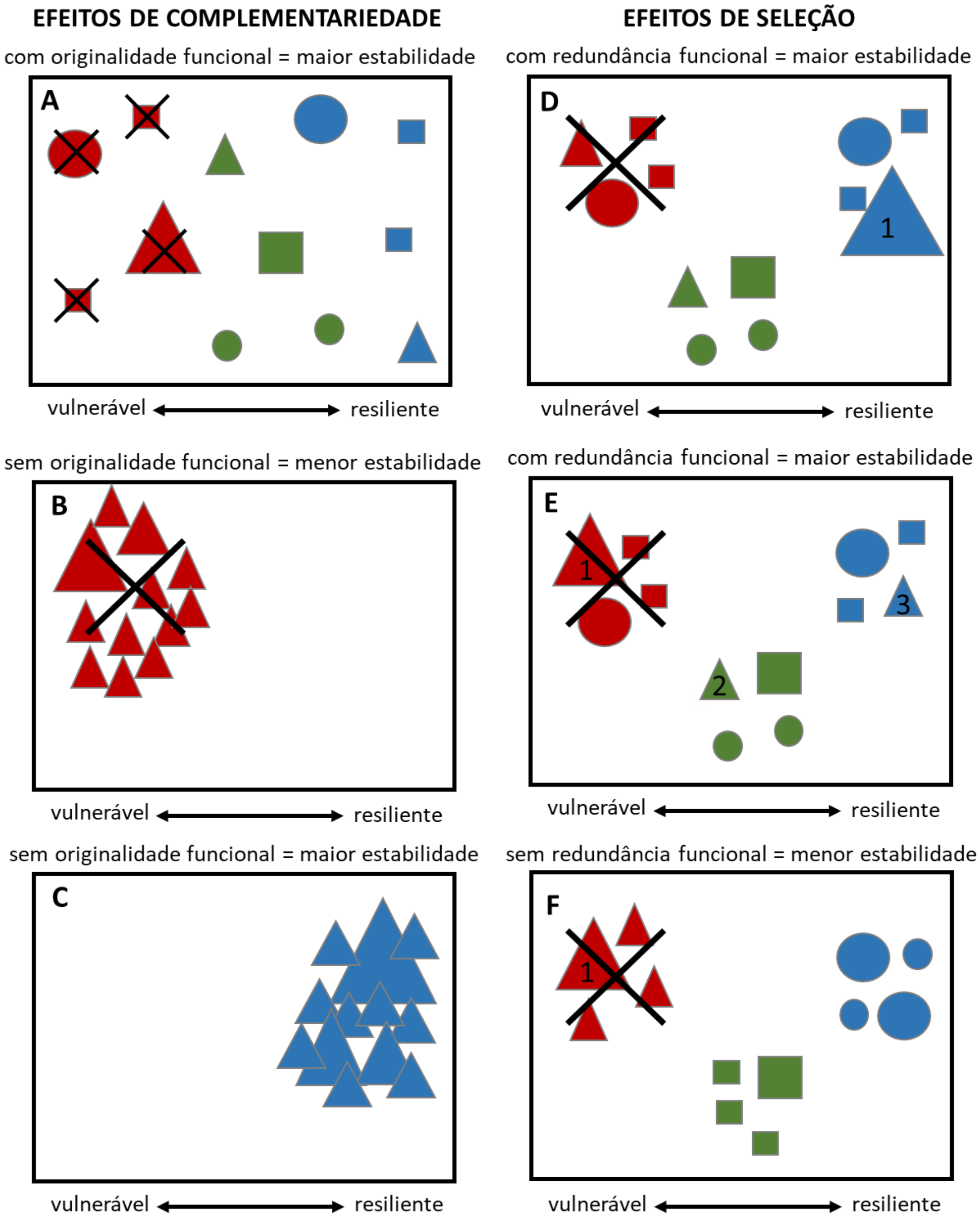
Os efeitos de complementariedade ocorreriam pois quanto maior a diversidade, maior a probabilidade de a comunidade incluir uma combinação de espécies complementares, em relação à captação e uso dos recursos, as quais seriam capazes de manter o funcionamento da comunidade mesmo sob distúrbio e/ou estresse (Hooper et al. 2005). Esse efeito está relacionado com a hipótese de partição de nicho (*'niche partitioning'* Macarthur e Levins 1967), segundo a qual, a separação espaço-temporal entre o nicho das espécies que compõem uma comunidade poderia aumentar a quantidade total de recursos disponíveis, reduzir a competição, e, consequentemente, possibilitar a coexistência entre as espécies. Por exemplo, comunidades mais diversas poderiam conter uma combinação de espécies com diferentes profundidades radiculares, de modo que a água poderia ser obtida tanto das camadas mais superficiais como das camadas mais profundas do solo. Essa complementariedade espacial na absorção de água poderia assegurar uma maior estabilidade na produção de biomassa durante um evento de seca, quando comparada a uma comunidade na qual todas as espécies possuem a mesma arquitetura radicular e competem mais pela água (Hoekstra et al. 2015). Segundo o efeito de complementariedade, a maior diversidade de espécies poderia contribuir para uma maior estabilidade ao proporcionar uma maior originalidade funcional. Isto é, a maior diversidade de espécies levaria a uma maior chance de a comunidade conter espécies ocupando diferentes porções do espaço funcional e respondendo de maneiras distintas aos distúrbios e/ou estresses (Hooper et al. 2005) (maior originalidade = maior estabilidade; Figura 3A); em comparação com uma comunidade em que a originalidade é baixa e todas as espécies respondem de maneira similar (menor originalidade = menor estabilidade; Figura 3B). É importante ressaltar que essa relação positiva entre originalidade e estabilidade não é, contudo, universal. Em alguns casos, maior originalidade poderia resultar em menor estabilidade. Por exemplo, se a alta complementariedade na captação e uso da água, ao invés de aumentar a disponibilidade total do recurso no sistema, acabasse provocando o seu esgotamento mais rápido (De Boeck et al. 2008, Grossiord et al. 2014); bem como menor originalidade poderia resultar em maior estabilidade, como no exemplo da Figura 3C, em que a originalidade é baixa porque todas as espécies são resilientes.

Efeitos de seleção, por sua vez, ocorreriam, pois quanto maior a diversidade de espécies, maior a probabilidade de que pelo menos uma delas irá responder favoravelmente ao distúrbio, sendo capaz de compensar eventuais perdas e de manter o funcionamento e a estabilidade da comunidade (Hooper et al. 2005). Ao enfatizar que uma espécie em particular poderia ser a responsável por controlar a estabilidade da comunidade, os efeitos de seleção estabelecem um paralelo com a hipótese da proporcionalidade de massas (‘*mass-ratio hypothesis*’ Grime 1998). De acordo com essa hipótese, o funcionamento das comunidades é largamente determinado pelas características das espécies dominantes, ou seja, pelas características das espécies que tem uma maior contribuição relativa para a biomassa total da comunidade (Grime 1998). Assim, unificando-se esses dois conceitos, seleção e proporcionalidade de massas, seria esperado que comunidades dominadas por espécies resilientes à seca exbissem alta estabilidade na produção de biomassa (Figura 3D). Já comunidades dominadas por espécies sensíveis a seca, exibiriam inicialmente baixa estabilidade, devido a grande perda de biomassa com a eliminação das espécies dominantes. Após a seca, a comunidade poderia exibir resiliência, se ao menos uma das espécies, até então subordinadas (i.e. espécies com baixos valores relativos de biomassa), fosse capaz de compensar a biomassa perdida, assumindo o papel de nova dominante (Figura 3E). Nesse cenário, uma maior diversidade de espécies contribuiria para uma maior estabilidade ao proporcionar um maior grau de redundância funcional (Naeem 1998, Walker 1992). A redundância funcional ocorre, portanto, quando há duas ou mais espécies que tem efeitos similares na comunidade; mas, diferem quanto as suas respostas aos distúrbios e/ou estresses. No exemplo acima, há redundância funcional, entre as espécies dominante e subordinada, as quais podem ter efeitos similares para a produção de biomassa, embora difiram na sua resposta (grau de resiliência) à seca (Hooper et al. 2005, Lavorel e Garnier 2002, Oliver et al. 2015). Porém, se as espécies fossem similares tanto no efeito quanto na resposta, a redundância seria basicamente o oposto da originalidade, e não necessariamente asseguraria maior estabilidade às comunidades (Suding et al. 2008). Pelo contrário, se houvesse uma completa sobreposição entre efeito e resposta, e as espécies respondessem negativamente ao distúrbio, a perda dessas espécies acarretaria necessariamente na perda de função; e, consequentemente, em menor estabilidade da comunidade (Figura 3F).

Complementariedade e seleção não são mecanismos mutuamente exclusivos. Ao promoverem, respectivamente, maior originalidade e maior redundância funcional, eles podem atuar em conjunto para aumentar a estabilidade dos sistemas biológicos (Oliver et al. 2015, Schmid et al. 2001). Além disso, embora tanto a originalidade quanto a redundância tendam a aumentar com o aumento do número de espécies (i.e. diversidade taxonômica), a causa final dos efeitos de complementariedade e de seleção, não é o número de espécies *per se*; mas, a existência de diversidade de resposta e de efeito entre as espécies (i.e. diversidade funcional) (Díaz e Cabido 2001, Heemsbergen et al. 2004, Hooper et al. 2005). Se todas as espécies respondessem da mesma maneira e exercessem efeitos similares, o número de espécies teria pouca ou nenhuma influência sobre a estabilidade. Essas relações se estabelecem, justamente, porque as plantas exibem uma enorme variedade de respostas à seca (Chaves et al. 2003, Farooq et al. 2009, Mitchell et al. 2015).

A abordagem funcional se propõe a caracterizar essas diferentes respostas, e se apresenta, portanto, como uma poderosa ferramenta para se obter explicações mais mecanicistas dos processos que regulam a estabilidade das comunidades e, consequentemente, para se predizer os impactos da seca sobre o seu funcionamento (Díaz e Cabido 2001, Kimball et al. 2016, Skelton et al. 2015). Caracterizar as respostas das plantas à seca, porém, não é uma tarefa fácil. Essas respostas operam em diferentes escalas temporais (de instantânea a evolutiva) (Felton e Smith 2017, Mitchell et al. 2015) e espaciais (do genoma ao indivíduo como um todo) (Chaves et al. 2003, Weltzin et al. 2003); e, por isso, envolvem alterações simultâneas em múltiplas características (fenológicas, morfológicas, anatômicas e fisiológicas); as quais frequentemente se encontram intercorrelacionadas devido a existência de '*trade-offs*' e restrições filogenéticas (Pivovaroff et al. 2016, Silvertown et al. 2015, West et al. 2012). Diante dessa complexidade, o grande desafio da abordagem funcional tem sido identificar e validar um conjunto de características funcionais (i.e. características fenológicas, morfológicas, anatômicas e/ou fisiológicas mensuradas no nível de indivíduo que tem impactos diretos ou indiretos sobre o sucesso reprodutivo dos organismos; e que descrevem o modo como eles respondem às condições ambientais (características de resposta) e/ou o modo como eles afetam os processos ecossistêmicos (características de efeito) (Violle et al. 2007, Lavorel e Garnier 2002) que seja, de fato, adequado para descrever as diferentes estratégias de resposta à seca (Funk et al. 2016, Rosado et al. 2013). A escolha dessas característicass sempre envolve um balanço entre acurácia de predição *versus* facilidade de mensuração. Em geral, as características que influenciam diretamente no desempenho dos indivíduos e que, portanto, tem alto poder preditivo, são de difícil mensuração ('*hard traits*'); já as características de fácil mensuração ('*soft traits*'), que podem ser rapidamente obtidas para um grande número de espécies, usualmente tem baixa capacidade preditiva (Griffin-Nolan et al. 2018).

Figura 3 - Diagrama conceitual demonstrando como os efeitos de seleção e de complementariedade, ao gerarem maior redundância e originalidade funcional, respectivamente, podem promover estabilidade nas comunidades.



Legenda: (A) a (C) - efeitos de complementariedade: uma maior diversidade de espécies contribuiria para uma maior estabilidade ao proporcionar um maior grau de originalidade funcional (i.e. existência de espécies que ocupam diferentes posições no espaço funcional); No cenário (A) a originalidade é alta, pois as espécies diferem na resposta (resiliência) à seca, o que resulta em maior estabilidade; No cenário (B) a originalidade é baixa, pois todas as espécies exibem a mesma resposta à seca, todas são sensíveis, o que resulta em menor estabilidade; No cenário (C) a originalidade é baixa, pois todas as espécies exibem a mesma resposta à seca; mas como são todas resilientes a estabilidade é maior; (D) a (F) - efeitos de seleção: uma maior diversidade de espécies contribuiria para uma maior estabilidade ao proporcionar um maior grau de redundância funcional (existência de espécies que exercem efeitos similares sobre os processos ecossistêmicos, mas diferem na sua resposta aos distúrbios e/ou estresses); No cenário (D) a espécie dominante (1) é resiliente à seca, o que resulta em maior estabilidade; No cenário (E) apesar da espécie dominante (1) ser sensível a seca, a existência de espécies subordinadas redundantes (2 e 3) poderia assegurar a estabilidade da comunidade; No cenário (F) as espécies são redundantes tanto em efeito, quanto em resposta; logo, se a espécie dominante (1) fosse perdida, não haveria espécies subordinadas capazes de substituí-la em suas funções, resultando em menor estabilidade. Todos os cenários compreendem o mesmo número de espécies (N = 12) para

enfatizar que não é número de espécies *per se* (diversidade taxonômica) mas a diversidade de respostas e efeitos das espécies (diversidade funcional) que determinam a relação entre diversidade e estabilidade. Nos diagramas acima cada ponto representa uma espécie; o tamanho do ponto reflete a biomassa relativa (pontos maiores representam espécies com maior contribuição relativa para a biomassa total da comunidade); os diferentes formatos refletem os grupos de efeito (i.e. pontos com mesmo formato representam espécies que exercem efeitos similares sobre os processos ecossistêmicos) e as cores indicam os grupos de resposta (i.e. pontos com mesma cor representam espécies que respondem de forma similar à seca). As espécies se distribuem no espaço funcional (i.e. espaço multidimensional definido por um conjunto de características funcionais) de acordo com o seu conjunto particular de características de resposta à seca. Espécies localizadas à direita no espaço funcional exibem características que lhes confere maior resiliência à seca. Já as espécies localizadas à esquerda são mais sensíveis, e seriam potencialmente eliminadas da comunidade em resposta a um evento de seca (por isso, estão marcadas com um X).
Fonte: O autor, 2019.

Justamente devido a facilidade de mensuração, características morfológicas das folhas, como área foliar (i.e. área total de um dos lados de uma folha, LA), área foliar específica (i.e. área foliar dividida pela massa seca da folha, SLA), e conteúdo de massa seca foliar (i.e. massa seca da folha dividida pela massa fresca, LDMC), inicialmente propostas para descrever a estratégia das plantas em termos de assimilação e alocação de carbono e para posicioná-las ao longo do espectro foliar econômico (i.e. *'leaf economic spectrum'*- LES, Wright et al. 2004), também tem sido amplamente utilizadas na tentativa de inferir a resposta das plantas à seca (Griffin-Nolan et al. 2018, Reich 2014). Por exemplo, essas três características, em conjunto, podem ser utilizadas para classificar as espécies de acordo com as estratégias ecológicas de competição, tolerância ao estresse e ruderalidade, propostas pela teoria do triângulo CSR (Grime 1977, Pierce et al. 2017). Segundo essa teoria, espécies tolerantes ao estresse são organismos pequenos (menor LA), que exibem um ciclo de vida longo, crescimento lento, e características econômicas foliares relacionadas ao uso conservativo dos recursos (menor SLA, maior LDMC); logo, se submetidas à seca elas responderiam através de um uso conservativo da água. Já as ruderais são organismos pequenos (menor LA), com ciclo de vida curto, crescimento rápido e uma estratégia aquisitiva de recursos (maior SLA, menor LDMC); em resposta à seca elas investiriam no crescimento reprodutivo (produção de sementes) para assegurar uma rápida recuperação após o distúrbio. Por fim, as espécies competidoras são organismos grandes (maior LA) com ciclo de vida longo e crescimento intermediário. Elas exibem também uma estratégia aquisitiva de recursos (maior SLA, menor LDMC); mas, em resposta à seca, ao invés de investirem na produção de sementes, elas investiriam na maximização da captação de água para manutenção do crescimento vegetativo (Grime 1977, 2002, Pierce et al. 2013, 2017).

Volaire et al.(2018) salientam as respectivas similaridades entre as estratégias de competição, tolerância ao estresse e ruderalidade, com as clássicas estratégias de evitação à desidratação (i.e. manutenção de altos potenciais hídricos mesmo sob condições de seca), escape à desidratação (i.e. regeneração após o evento de seca) e tolerância (i.e. que inclui tanto tolerância à desidratação: plantas capazes de manuter o funcionamento fisiológico, até certo grau, mesmo sob baixos potenciais hídricos na planta; quanto tolerância à dessecação: plantas capazes de equalizar o conteúdo hídrico foliar em relação à umidade atmosférica ambiente e também capazes de recobrar as atividades fisiológicas após reidratação, mesmo depois de longos períodos desidratadas)(Levitt 1972).

Essas similaridades resultariam de uma convergência funcional, no nível do indivíduo como um todo, em relação a estratégia de captura e uso dos recursos. Isto é, organismos com uma estratégia conservativa, seriam conservativos no uso e captura de todo e qualquer tipo de recurso; do mesmo modo que organismos aquisitivos o seriam, independentemente do recurso em questão (Reich et al. 2014). Sendo esse pressuposto válido, então as características econômicas morfológicas, de fácil mensuração, poderiam ser utilizadas para descrever as respostas das plantas à limitação em qualquer tipo recurso: luz, nutrientes ou água [e os ecólogos funcionais teriam uma vida mais fácil] (Reich et al. 2014).

Contudo, em seu recente artigo de revisão, Griffin-Nolan et al. (2018) argumentam contra esse pressuposto. Segundo esses autores, como as características econômicas raramente variam de modo predizível ao longo de gradientes de disponibilidade de água, elas não seriam adequadas para descrever e predizer a resposta das plantas à seca. Ao invés de características econômicas, as estratégias de resposta à seca deveriam ser descritas pelo uso de características hidráulicas, como condutância estomática, potencial hídrico, potencial hídrico no ponto de perda de turgor, vulnerabilidade do xilema à cavitação, entre outras. Essas características hidráulicas seriam melhores descritoras, pois além de variarem de modo predizível ao longo de gradientes de precipitação (e.g. Blackman et al. 2012), elas estão mecanisticamente relacionadas com o modo como as plantas obtem, transportam e utilizam a água; e, portanto, elas refletem a capacidade das plantas em lidar com condições de baixa disponibilidade hídrica (Brodribb 2017). A desvantagem, todavia, é que a maior parte dessas características exigem procedimentos laboratoriais laboriosos e/ou o uso de equipamentos sofisticados para a sua mensuração, o que dificulta a sua obtenção para um grande número de espécies [e torna a vida dos ecólogos funcionais mais difícil] (Griffin-Nolan et al. 2018).

Uma vez que a estabilidade depende não só da capacidade das plantas resistirem (tolerarem e/ou evitarem) à seca, mas também da sua capacidade de recuperação após o distúrbio (escape), características diretamente relacionadas a processos regenerativos (e.g. tamanho e massa das sementes, taxa de germinação, síndrome de dispersão, capacidade de rebrota) também deveriam ser consideradas (Lavorel 2007, Lavorel e Pausas 2003, Mcintyre et al. 1999); o que raramente tem sido feito (Mitchell et al. 2015). Por fim, a descrição das estratégias de resposta à seca, de modo geral, tem se restringido ao modelo unidirecional do contínuo solo-planta-atmosfera (SPAC), e considerado o solo como fonte exclusiva de água para as plantas. No entanto, já existe ampla evidência de que, especialmente durante eventos de seca, as plantas podem se utilizar de fontes alternativas de água. Por exemplo, elas podem absorver água da neblina através das folhas, e redistribuí-la para as raízes, transportando água no sentido reverso ao previsto pelo SPAC (Goldsmith et al. 2013). Assim, para se desvendar o efeito da diversidade funcional na resposta das plantas à seca, seria preciso avaliar simultaneamente múltiplas características funcionais (econômicas, hidráulicas e regenerativas), a fim de se compreender como elas se relacionam entre si (*trade-offs*), e quais delas constituem as melhores descritoras das diferentes estratégias de resposta à seca (Pérez-Ramos et al. 2013). Além disso, a capacidade das plantas absorverem água de fontes atmosféricas, deveria ser incluída nessa abordagem (Yang et al. 2010), tornando-se necessário identificar e validar novas características funcionais capazes de descrever o efeito das fontes alternativas de água na resposta das plantas à seca (Rosado e Holder 2013).

O efeito das fontes alternativas de água

Se as raízes não conseguem absorver a quantidade de água suficiente para suprir a demanda metabólica, algumas plantas podem se valer de fontes atmosféricas de água, como neblina e/ou orvalho, para manter o seu balanço hídrico (e.g. Agam e Berliner 2006, Goldsmith et al. 2013, Limm et al. 2009). Uma alta umidade relativa do ar pode amenizar os efeitos negativos da seca basicamente de três modos distintos (Goldsmith 2013). Primeiramente, a presença de uma atmosfera saturada de vapor de água reduz a demanda evaporativa do ar (decréscimo no VPD), de modo que as plantas perdem menos água por transpiração (e.g. Goldsmith et al. 2013, Limm et al. 2009). Em segundo lugar, as partículas de água suspensas na atmosfera podem ser interceptadas pelas plantas e, em seguida, escoadas para o substrato, aumentando o conteúdo de água disponível nas camadas superficiais do solo (e.g. Bruijnzeel et al. 2011, Carbone et al. 2013), fenômeno denominado de precipitação oculta ou horizontal (*fog drip*) (Ewing et al. 2009). Por fim, o terceiro modo pelo qual as plantas podem se utilizar da água atmosférica é através da absorção foliar da água *(foliar water uptake,* FWU) (Goldsmith 2013). Acredita-se que o FWU ocorre de forma passiva, a favor de um gradiente de potencial hídrico, que se estabelece entre a atmosfera saturada de vapor de água e os tecidos foliares (Rundel 1982). A neblina e/ou o orvalho condensam-se sobre a superfície foliar e são, então, absorvidos na forma líquida, ou pode até mesmo ocorrer a absorção da água sobre a forma de vapor (Berry et al. 2018, Vesala et al. 2017).

O FWU pode ser favorecido pela presença de estruturas especializadas, como tricomas e hidatódeos (Martin e Von Willert 2000). Mas, na ausência destas, a entrada de água também pode ocorrer através da cutícula, ou até mesmo pelos estômatos (Burkhardt 2010, Eller et al. 2013, Gouvra e Grammatikopoulos 2003). A água absorvida pode ser utilizada na fotossíntese ou em outras atividades metabólicas, reduzindo os efeitos negativos da seca sobre a sobrevivência, crescimento e reprodução das plantas (Eller et al. 2013, Goldsmith et al. 2013; Simonin et al. 2009). Análises isotópicas permitiram determinar que, durante eventos extremos de seca, a umidade atmosférica pode contribuir com até 42% do conteúdo de água das folhas (Eller et al. 2013), constituindo a principal, ou mesmo a única, fonte de água para as plantas (Agam e Berlim 2006). Sob condições de alta umidade atmosférica e baixa disponibilidade hídrica no solo, a água absorvida pelas folhas poderia inclusive ser transportada até as raízes, e destas para o solo circundante, tornando-se disponível para as espécies vizinhas (Nadezhdina et al. 2010).

O FWU parecer ser um fenômeno ubíquo, uma vez que já foi relatado em pelo menos 233 espécies de 77 diferentes famílias botânicas (Berry et al. 2018). Porém, vários estudos apontam a existência de uma grande variação interespecífica na quantidade de água absorvida (Fu et al. 2015, Goldsmith et al. 2013, Limm et al. 2009). Isso significa que nem todas as espécies dentro de uma comunidade se beneficiam de fontes atmosféricas de água da mesma maneira (Goldsmith et al. 2013). Há evidências de que a variação no FWU pode estar associada com a forma de vida e fenologia das plantas (Fu et al. 2015); e com as suas características foliares, tanto morfológicas, (espessura e suculência, Gotsch et al. 2015) como fisiológicas (condutância estomática, potencial hídrico, e comportamento iso-anisohídrico, Berry et al. 2014, Breshears et al. 2008, Eller et al. 2016, Gotsch et al. 2015). Além disso, propriedades químicas (composição cuticular) e estruturais (estômatos, tricomas, rugosidades) da superfície foliar, ao influenciarem no grau de retenção e repelência da água sobre a folha, bem como na sua permeabilidade à entrada e saída de água, também poderiam ser fatores importantes para explicar essa variação (Fernández et al. 2017, Oliveira et al. 2014). Esses resultados, contudo, foram obtidos através do estudo de um limitado número de características funcionais, mensuradas num limitado número de espécies. Avaliações no nível de comunidade, englobando um maior número de espécies co-ocorrentes, são ainda necessárias para se identificar quais os fatores e condições que, de fato, favorecem o FWU. Esse conhecimento é importante, primeiramente, para melhor esclarecer quais os mecanismos fisiológicos que possibilitam a entrada e o transporte de água dentro da folha; e, em segundo lugar, para melhor compreender quais as implicações ecológicas do FWU, especialmente considerando o contexto de mudanças climáticas (Berry et al. 2018, Eller et al. 2016, Goldsmith et al. 2013, Qiu et al. 2010). Num primeiro momento, a capacidade das plantas utilizarem fontes alternativas de água durante eventos de seca poderia constituir uma vantagem ecológica, considerando as previsões de que as secas se tornarão mais intensas, frequentes e duradouras. Porém, essa estratégia pode acabar se mostrando desvantajosa, uma vez que vários modelos climáticos preveem também uma redução na frequência e intensidade dos eventos de neblina; particularmente em regiões montanhosas, em decorrênciada elevação na altitude média de formação das nuvens (Pounds et al. 1999, Still et al. 1999).

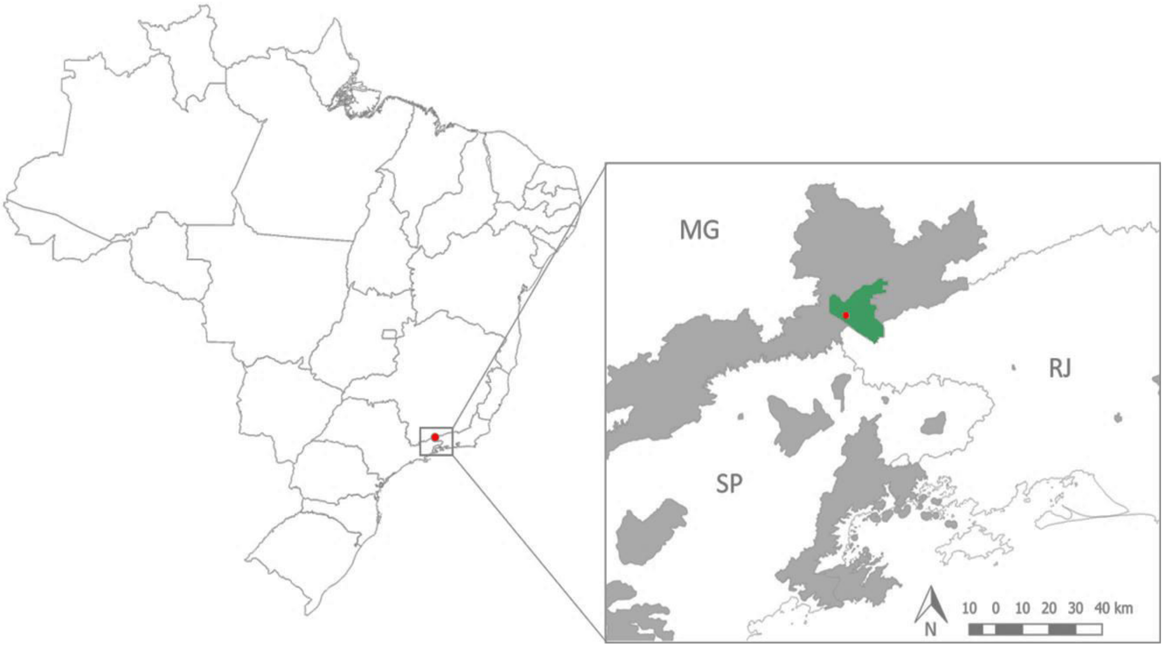
Modelo de estudo e espécies avaliadas

As regiões montanhosas constituem um ambiente singular para o estudo do efeito da diversidade funcional e das fontes alternativas de água na resposta da vegetação à seca. Primeiramente, devido ao isolamento geográfico, à migração altitudinal e ao alto grau de endemismo e especialização das espécies, as vegetações montanhosas são consideradas como potencialmente vulneráveis às mudanças climáticas (Assis e de Mattos 2016, Beniston 2003). Em segundo lugar, a sazonalidade na distribuição das chuvas, combinada à presença de um substrato rochoso com uma topografia complexa, que pode tanto facilitar quanto impedir, a retenção de água, favorece o desenvolvimento de distintas estratégias funcionais de resposta à seca (Kluge e Budel 2008, Porembski e Barthlot 2000); resultando, por exemplo, na coexistência, lado a lado, de espécies suculentas (estratégia de evitação); geófitas (estratégia de escape) e tolerantes à dessecação (estratégia de tolerância). Além disso, a neblina constitui um importante fator ecohidrológico. Particularmente nas montanhas tropicais, a frequência e a intensidade dos eventos de neblina podem afetar tanto o suprimento (i.e. precipitação oculta e FWU) quanto a demanda (i.e. redução da evapotranspiração) de água; e, consequentemente, podem influenciar a composição e o funcionamento das comunidades vegetais e as suas respostas aos eventos de seca (Aparecido et al. 2018, Bruijnzeel et al. 2011). Por fim, as vegetações montanhosas exibem um alto valor biológico; pois abrigam um grande número de espécies endêmicas e ameaçadas de extinção; bem como um alto valor socio-econômico, pois abrigam diversas nascentes que constituem uma importante fonte de água potável para a população humana (Safford 1999).

Por todos esses motivos, os Campos de Altitude (também chamados de Páramos ou *Brazilian high altitude grasslands*), formações herbáceo-arbustivas características dos cumes de montanha do sul e sudeste brasileiro (Safford 1999), foram escolhidos como sistema modelo para a realização desse estudo. Os Campos de Altitude constituem um dos ecossistemas associados ao bioma Mata Atlântica (Brasil 2008) e ocorrem entre os estados de Santa Catarina e Espírito, em altitudes acima de 1.800 metros, compreendendo uma extensão total original de cerca de 350 km² (Safford 1999). O presente trabalho foi desenvolvido especificamente nos Campos de Altitude do Parque Nacional do Itatiaia (PNI), primeira unidade de conservação do Brasil, fundada no ano de 1937, e localizada na porção central da Serra da Mantiqueira, entre os municípios de Itatiaia (RJ) e Itamonte (MG)(Figura 4).

Essa região possui um clima tropical de altitude (Cwb - Köppen), com temperatura média anual de 14,4 °C e precipitação média anual de 2.000 e 2.200 mm (Segadas-Vianna e Dau 1965). Temperaturas abaixo de 0 ºC são comuns nas noites de inverno (podendo atingir até -15 °C), resultando numa ocorrência média de 56 geadas por ano (Segadas-Vianna e Dau 1965). Em relação a precipitação, há uma forte sazonalidade na distribuição das chuvas. Estas se concentram durante os meses de verão (dezembro a março), com um período de estiagem de três meses (junho e agosto) durante o inverno, quando a precipitação média mensal se torna inferior a 50 mm (Safford 1999). Durante o período de estudo (junho 2016 a agosto de 2017), a temperatura média foi de 9 °C, a umidade relativa média do ar foi de 85 % e a precipitação média de 155 mm mensais (Figura 5).

Figura 4 - Localização da área de estudo



Legenda: a área de estudo está indicada pelo ponto vermelho (22°22'24,3"S 44°42'16,9"O; 2.400 m asl), e está inserida na unidade de conservação federal do Parque Nacional do Itatiaia (PNI, em verde). O PNI está localizado na divisa entre os estados do Rio de Janeiro (RJ), Minas Gerais (MG) e São Paulo (SP). As áreas em cinza delimitam outras unidades de conservação federais presentes nesses estados.
Fonte: O autor, 2019.

Modelos de mudanças climáticas para os Campos de Altitude da região sudeste do Brasil preveem aumentos significativos nas temperaturas médias anuais (entre 1,8 e 2,6 ºC) e aumentos pouco expressivos na precipitação média anual (entre 25,22 e 109,72 mm) até o ano de 2050 (Assis e de Mattos 2016). As projeções específicas para a área de estudo também apontam um aumento na temperatura média anual (entre 1,7 e 2,5 ºC) e na precipitação média anual (entre 111 a 219 mm), uma redução na sazonalidade da precipitação (entre -6 e -7), e um aumento pouco expressivo na precipitação durante o mês mais seco (entre 8 e 12 mm) (Tabela 1). Porém, as previsões são distintas em relação a precipitação no mês mais chuvoso, podendo haver tanto aumento, quanto redução na quantidade de chuvas, dependendo do cenário de emissão de gases considerado (Tabela 1). Apesar das previsões de aumento na precipitação média, a região pode ficar sujeita a ocorrência de secas mais extremas. Especialmente durante anos sobre influência do El niño, nos quais os invernos tendem a ser mais secos, bem como tendem a ocorrer períodos anormais de estiagem durante o verão, os chamados veranicos (Safford 1999). O aumento da temperatura média, e, consequentemente da demanda evaporativa do ar (Leuschner 2000) somados a redução na frequência dos eventos de neblina e a intensa inclinação do relevo (Pounds et al. 1999, Safford 1999) podem intensificar a transformação de um déficit de precipitação em um déficit hídrico no solo dos Campos de Altitude. Longos períodos de estiagem também estão frequentemente associados a ocorrência de incêndios, na maioria das vezes de origem antrópica, que constituem uma das principais ameaças à vegetação dos Campos de Altitude (Aximoff e Rodrigues 2011)

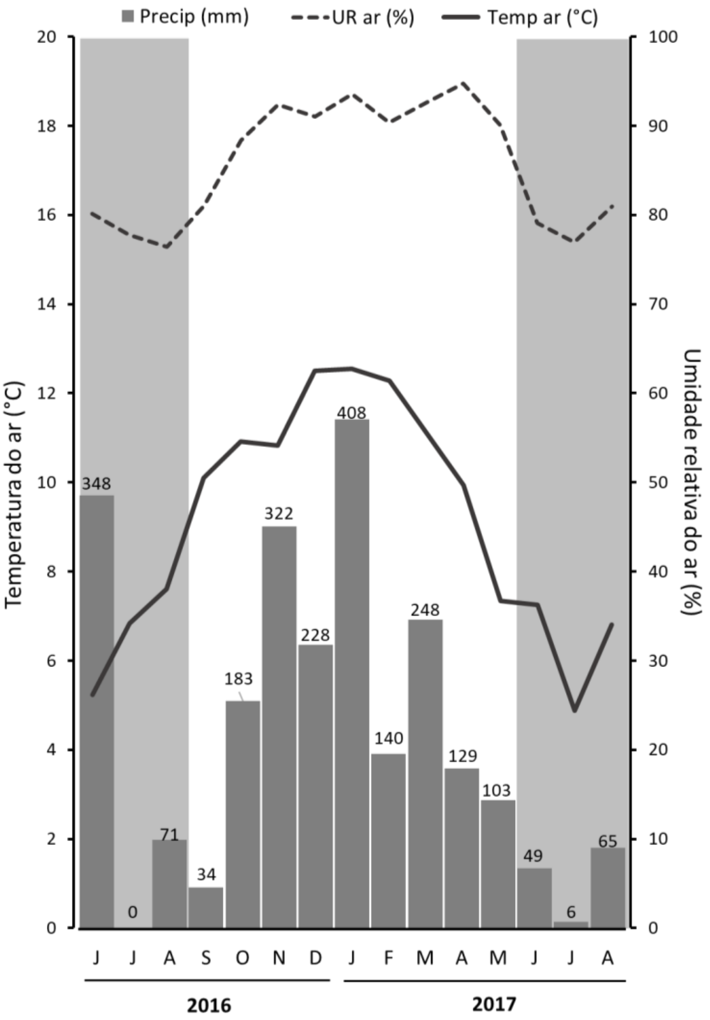
Tabela 1 - Previsões de mudanças na temperatura e no regime de precipitação para a área de estudo – Campos de Altitude do Parque Nacional do Itatiaia (22°22'24,3"S 44°42'16,9"O) no ano de 2050 segundo o modelo de circulação geral HAdGEM2-ES, considerando os cenários mais otimista (RCP 2,6) e mais pessimista (RCP 8,5) de emissão de gases segundo o IPCC (2013).

Variável bioclimática	**Presente**	**HadGEM2**	
		RCP 2.6	**RCP 8.5**
Temperatura média anual (°C)	10,2	1,7	2,5
Precipitação anual (mm)	2.296,0	111,0	219,0
Precipitação do mês mais chuvoso (mm)	388,0	-30,0	11,0
Precipitação do mês mais seco (mm)	38,0	12,0	8,0
Sazonalidade da precipitação (cv)	69,0	-7,0	-6,0

Legenda: as variáveis bioclimáticas temperatura média anual (°C), precipitação total anual (mm), precipitação do mês mais chuvoso (mm), precipitação do mês mais seco (mm) e sazonalidade da precipiração (coeficiente de variação) foram obtidas através do WorldClim (http://www. worldclim.org/) em dois recortes temporais, um no presente (1970-2000) e outro para o ano de 2050, ambas na resolução de 30”(aproximadamente 1 km²). As cinco variáveis bioclimáticas futuras foram geradas a partir do modelo de circulação geral, o ‘Met Office Hadley Centre’ - HadGEM2- ES. As mudanças das variáveis foram medidas através da diferença dos valores de cada variável nos dois recortes temporais. De modo que valores negativos/positivos indicam reduções/aumentos no futuro em comparação com o presente. As análises foram realizadas através do programa QGIS.

Fonte: O autor, 2019.

Figura 5 - Médias mensais de temperatura (°C) e umidade relativa do ar (%) e precipitação acumulada para a área de estudo (Campos de Altitude do Parque Nacional do Itatiaia, Rio de Janeiro, Brasil), durante o período de estudo (junho de 2016 a agosto de 2017).

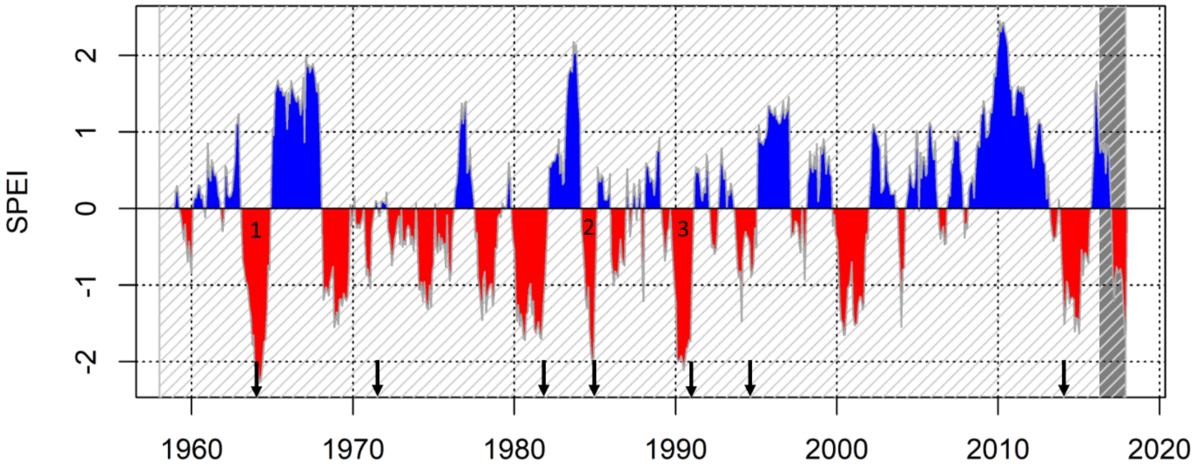


Legenda: registros diários (a cada 15 min) de temperatura (°C) e umidade relativa do ar (%) foram obtidos a partir de uma estação meteorológica localizada aproximadamente 15 km da área de estudo (22°25'33,6"S,44°34'26,4" O, 2.470m asl). Já os dados mensais de precipitação foram obtidos a partir de um pluviômetro instalado a cerca de 300 metros da área de estudo (22°22'27,8"S, 44°42'07,9" O). Áreas em cinza indicam a estação seca (junho a agosto).

Fonte: O autor, 2019.

A Figura 6 apresenta os valores de SPEI (índice padronizado de precipitação evapotranspiração) para a área de estudo entre os anos de 1958 a 2017. O SPEI é um índice utilizado para estimar a intensidade dos eventos de seca, sendo que valores negativos/positivos indicam períodos mais secos/úmidos do que o normal (Vicente-Serrano et al. 2010). Observa-se que o primeiro ano de estudo (2016) foi um pouco mais úmido do que o normal (SPEI médio 0,91), enquanto que o segundo ano (2017) foi mais seco (SPEI médio -0,95). Contudo, as condições climáticas durante ambos os anos ainda podem ser consideradas como dentro da normalidade para a área de estudo (i.e. -0,99 < SPEI <0,99 = condições normais). Na Figura 6, as setas indicam os anos sob forte influência do El niño, podendo-se notar que os três eventos de secas mais extremos (SPEI < -2,0) que afetaram a região, ocorreram, de fato, em anos sob forte influência desse fenômeno (1965-66; 1987-88 e 1991-92).

Figura 6 - Intensidade dos eventos de seca na área de estudo (Parque Nacional do Itatiaia, Rio de Janeiro, Brasil) durante o período de 1958 a 2017.



Legenda: os valores de SPEI foram calculados em ambiente R usando o pacote 'SPEI', com base numa escala temporal de 12 meses, e utilizando os dados mensais de precipitação (PPT) e de potencial de evapotranspiração (PET) obtidos a partir do banco de dados TerraClimate (Abatzoglou et al. 2018). O valor de SPEI representa o número de desvios padrões pelo qual o balanço hídrico climático (PPT - PET) diverge em relação a média histórica registrada para um dado local; e pode ser interpretado segundo a escala: extremamente seco SPEI < -2,00; severamente seco: -1,50 < SPEI < -1,99; moderadamente seco: -1,00 < SPEI < -1,49; condições normais: -0,99 < SPEI < 0,99; moderadamente úmido:1,00 < SPEI < 1,49; severamente úmido: 1,50 < SPEI <1,99; e extremamente úmido: SPEI > 2,00. A área cinza indica os dois anos de realização desse estudo (2016-2017); as setas indicam os anos sob forte influência do El niño; e os números (1-3) indicam eventos extremos de seca que ocorreram na região.

Fonte: O autor, 2019.

Devido a elevada altitude, as massas de ar úmidas de origem oceânica tendem a se resfriar, resultando em frequentes eventos de neblina na região (Safford 1999). A neblina poderia amenizar os efeitos negativos da seca; embora, até o momento, não haja nenhum estudo avaliando a capacidade das plantas dos Campos de Altitude de utilizarem esta fonte alternativa de água (Aparecido et al. 2018). De acordo com Segadas-Vianna e Dau (1965), em Itatiaia, os eventos de neblina ocorrem com uma frequência média de 218 dias por ano. Entre os anos de 2015 e 2016, eventos de neblina ocorreram em 32% dos dias. Em média, houve 10 dias de neblina por mês, com duração entre 1,6 horas e 46 horas (Figura 7A). Durante esse período foi observada uma sazonalidade na frequência e duração dos eventos de neblina, os quais foram menos frequentes e duradouros na estação seca (16% de dias com neblina por mês, 34 horas mensais de neblina), em comparação com a estação chuvosa (51% e 92 horas). Além disso, foi observada uma correlação positiva e significativa entre a porcentagem mensal de dias com neblina e a precipitação acumulada mensal (Spearman rank correlation: $\rho= 0,48$; $P = 0,028$; $R^2 = 0,15$), indicando menor frequência de eventos de neblina nos meses mais secos. Em termos de variação diária, os eventos de neblina foram mais frequentes de dia (do que durante a noite), especialmente no horário entre 8h e 9h da manhã (Figura 7B).

Os solos da área de estudo são, em geral, rasos, distróficos, com alta saturação de alumínio e baixa capacidade de troca catiônica (Benites et al. 2007). Predominam as classes neossoloslitólicos e cambissolos húmicos, derivados de rochas ígneas ou metamórficas, como granito, gnaisse e nefelino-sienito (Segadas-Vianna 1965). Durante o período de estudo a temperatura média do solo, à profundidade de 20 cm, foi de 11.5 °C (amplitude 6,9 - 16,7 °C), enquanto que o conteúdo volumétrico de água no solo foi em média de 0.44 m^3 m^{-3} (amplitude 0,27 - 0,63 m^3 m^{-3}) (Figura 8).

Esses solos sustentam uma vegetação composta por uma matriz de gramíneas e outras herbáceas, com alguns esparsos arbustos (Figura 9A); a qual recobre uma área total de 39 km² (cerca de 14% do PNI) (Giovanetti-Alves et al. 2016). A diversidade de espécies é considerável, com mais de 550 espécies de plantas vasculares identificadas, sendo 11% delas endêmicas do Planalto do Itatiaia, e 21% endêmicas dos Campos de Altitude (Giovanetti-Alves et al. 2016, Martinelli 2007). As famílias mais representativas são Poaceae, Cyperaceae, Asteraceae, Ericaceae, Melastomataceae e Verbenaceae (Camerik e Werger 1981). Entre as poáceas, destaca-se a espécie *Cortaderia modesta* (Döll.) Hack (cabeça de negro), que domina a matriz herbácea na maior parte dos Campos de Altitude. Em algumas áreas essa gramínea ocorre em associação com a ciperácea *Machaerina ensifolia* (Boeckeler) T. Koyama, de modo que os rizomas de ambas as espécies se entrelaçam e formam pseudotroncos, os quais podem alcançar mais de dois metros de altura (Brade 1956, Giovanetti-Alves et al. 2016; Figura 9B).

A fim de subsidiar a escolha das espécies a serem avaliadas neste estudo, foi realizado um levantamento de frequência (Coulloudon et al. 1996). Para tanto, 12 transectos de 100 metros foram estabelecidos na área de estudo e, em seguida, parcelas de 1m² foram alocadas ao longo de cada transecto. As parcelas foram alocadas a cada intervalo de 3 metros, totalizando 300 m² de área amostrada. Em cada parcela, foi contabilizada a presença/ausência de todas as espécies de plantas vasculares, e ao final, a frequência de cada espécies foi obtida como: frequência da espécie i = n° de parcelas em que a espécie i estava presente dividido pelo número total de parcelas. Ao final, foi escolhido um total de 76 espécies (Figura 10;

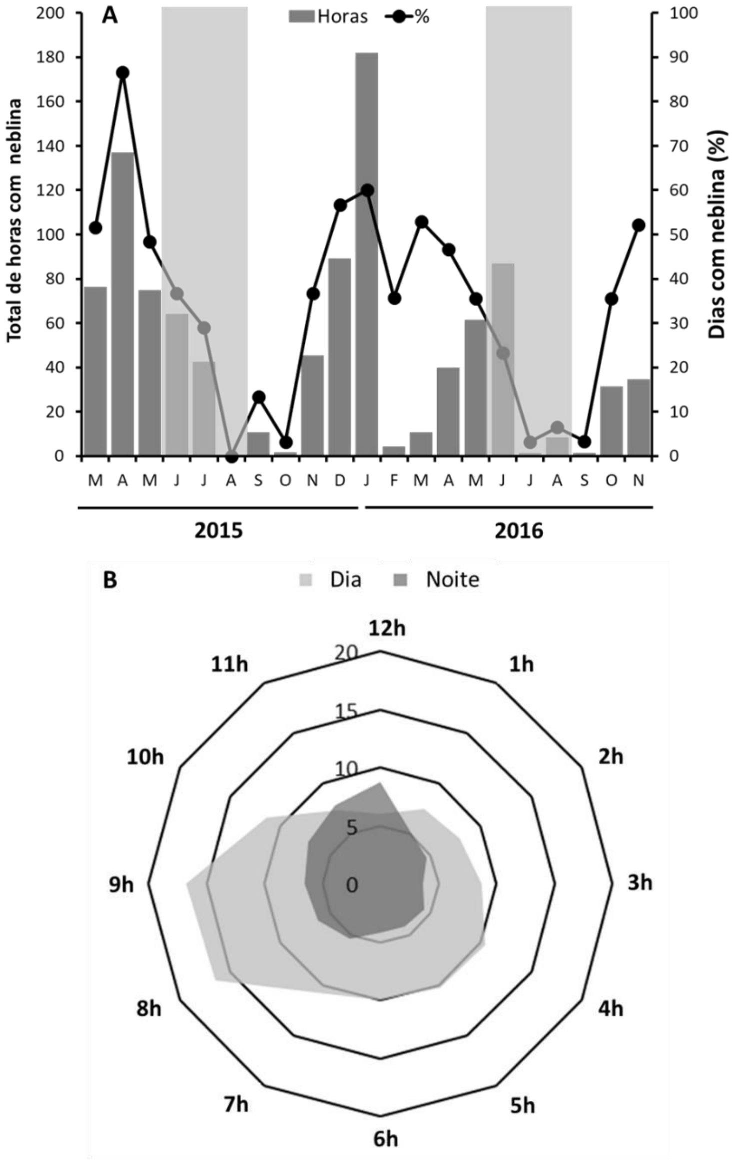
Apêndice), incluindo diferentes formas de vida (arbustos e ervas) e diferentes graus de frequência (raras e dominantes); as quais em conjunto representaram 84,8% da frequência total de espécies na comunidade.

Estruturação da tese

Este estudo encontra-se estruturado em três partes:

Na primeira parte, intitulada "*Deciphering ecological stability of grasslands productivity in response to experimental droughts*", foi realizada uma meta-análise de estudos reportando os efeitos de experimentos de manipulação de chuva sobre a biomassa aérea em 101 vegetações campestres ao redor do globo. Através dessa meta-análise foi possível determinar a importância relativa de diferentes fatores abióticos para explicar a variação no grau de estabilidade entre as vegetações. Além disso, foi avaliado como as três propriedades da estabilidade (resistência, recuperação e resiliência) se relacionam entre si, e qual a contribuição de cada uma delas para determinar a estabilidade geral das vegetações campestres em resposta às secas experimentais. Por fim, foram também discutidas algumas limitações conceituais e metodológicas dos experimentos de manipulação de chuva, e foram propostas importantes recomendações para futuros experimentos.

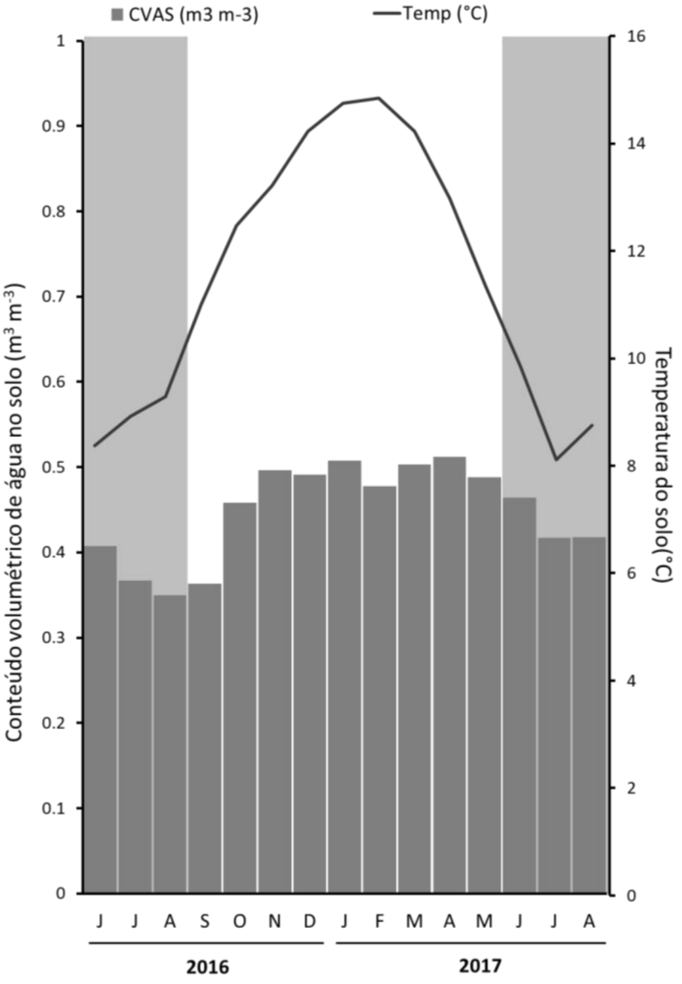
Figura 7 - Caracterização dos eventos de neblina para a área de estudo (Campos de Altitude do Parque Nacional do Itatiaia, Rio de Janeiro, Brasil), durante o período de março 2015 a novembro 2016.



Legenda: (A) -frequência (porcentagem de dias com neblina) e duração (total de horas de neblina) mensal dos eventos de neblina na área de estudo. Áreas em cinza demarcam a estação seca (junho a agosto);(B) - frequência horária média de ocorrência de eventos de neblina. A ocorrência de eventos de neblina foi determinada usando os registros diários (a cada 15 min) de temperatura (°C) e umidade relativa do ar (%) e de precipitação acumulada (mm),obtidos a partir de uma estação meteorológica localizada a aproximadamente 15 km da área de estudo (22°25’33,6”S,44°34’26,4” O, 2.470 m asl). Para tanto, o déficit de pressão de vapor (VPD) foi computado usando os dados de temperatura e umidade. Em seguida, foram considerados como eventos de neblina os intervalos de tempo nos quais o VPD estava próximo de zero, mas não havia registro de chuva pelo pluviômetro. Devido a problemas no pluviômetro da estação metereológica não foi possível determinar o VPD para o período exato de estudo (junho 2016 a agosto de 2017). Por isso, a ocorrência de neblina foi computada para o período de março de 2015 a novembro de 2016.

Fonte: O autor, 2019.

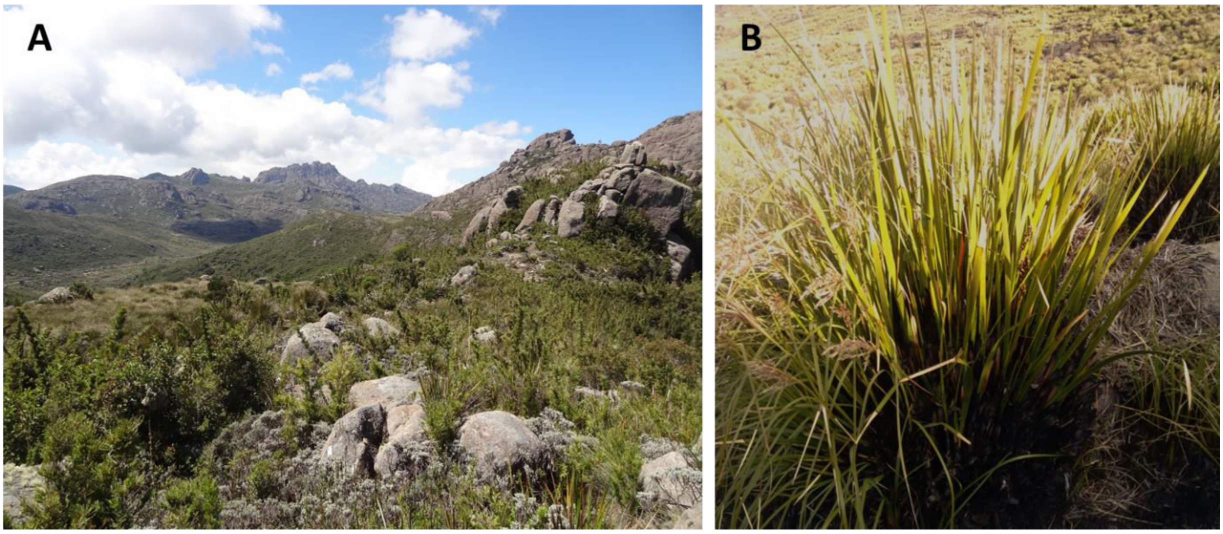
Figura 8 - Médias mensais de conteúdo volumétrico de água no solo (CVAS, m^3 m^{-3}) e temperatura do solo (°C) à profundidade de 20 cm na área de estudo (Campos de Altitude do Parque Nacional do Itatiaia, Rio de Janeiro, Brasil), durante o período de estudo (junho de 2016 a agosto de 2017).



Legenda: registros diários (a cada 10 minutos) do conteúdo volumétrico de água no solo e da temperatura do solo foram obtidos através de quatro sensores de solo (5TM soil moiusture and temperature sensor, Decagon Devices, SOIL Pullman, WA, USA) instalados na área de estudo (22º22’37” S, 44º42’28” O, 2.400 m asl) à profundidade de 20 cm. Áreas em cinza indicam a estação seca (junho a agosto).

Fonte: O autor, 2019.

Figura 9 - A vegetação dos Campos de Altitude do Parque Nacional do Itatiaia (Rio de Janeiro, Brasil).



Legenda: (A)- vista parcial da área de estudo, observando-se ao fundo o pico das Agulhas Negras; (B) -touceira formada pela associação entre as duas espécies co-dominantes nos Campos de Altitude do Parque Nacional do Itatiaia, *C. modesta* (à esquerda) e *M. ensifolia* (à direita).
Fonte: O autor, 2019.

Na segunda parte, intitulada "*Integrating eco-physiological strategies and functional originality indices to predict plant Community stability in response to droughts*", utilizou-se a vegetação de Campos de Altitude como um sistema modelo para avaliar o efeito da diversidade funcional na resposta das plantas à seca. Nesta parte, foi proposto uma abordagem integrando estratégias eco-fisiológicas e índices de originalidade funcional, como uma ferramenta para se prever os efeitos da seca sobre a vulnerabilidade das comunidades à homogeneização funcional (i.e. perda de diversidade funcional) e para se identificar espécies prioritárias para conservação. Essa abordagem é inovativa, uma vez que as estratégias de resposta à seca foram descritas através do uso simultâneo de características econômicas, hidráulicas e regenerativas; considerando, inclusive, características relacionadas com a capacidade das plantas utilizarem fontes alternativas de água.

Na terceira parte foi avaliado o efeito das fontes alternativas de água na resposta das plantas à seca, sendo este o primeiro estudo a investigar a capacidade das plantas dos Campos de Altitude de utilizarem fontes atmosféricas de água. Estaparte, inclui o artigo "*Who are the leaf water uptakers? Determining leaf traits that influence atmospheric water absorption by plants"* que apresenta um conjunto de características foliares capazes de explicar as variações interespecíficas no FWU; bem como discute as implicações ecológicas do FWU dentro do contexto das mudanças climáticas. A parte 3 inclui ainda o artigo intitulado “*Retain or repel? Droplet volume does matter when measuring leaf wetness traits*”, publicado no periódico *Annals of Botany* (doi: 10.1093/aob/mcw025), o qual aponta alguns problemas metodológicos e adverte para a necessidade de validação de características funcionais potencialmente relacionadas à capacidade das plantas de utilizarem fontes alternativas de água, como as características de retenção e repelência foliar de água.

Objetivos

Objetivo geral:avaliar o efeito da diversidade funcional e das fontes alternativas de água na estabilidade das comunidades vegetais em resposta à eventos de seca.

Objetivos específicos:

Parte 1. Fatores que influenciam a estabilidade de vegetações campestres em resposta à seca:
(1) Identificar quais índices têm sido utilizados para acessar a estabilidade das vegetações campestres em resposta à seca, e avaliar se diferentes índices produzem resultados comparáveis entre si ou não;
(2) Avaliar a estabilidade (resistência, resiliência e recuperação) das vegetações campestres em resposta à seca em termos de biomassa aérea;
(3) Identificar potenciais *trade-offs* entre as três propriedades da estabilidade;
(4) Quantificar a importância relativa das características da seca (intensidade, duração e frequência), das condições climáticas (sazonalidade da precipitação, precipitação média anual e temperatura média anual) e da altitude de cada área de estudo para explicar a variação na estabilidade entre as vegetações campestres.

Parte 2. O efeito da diversidade funcional:
(1) Descrever as estratégias eco-fisiológicas de resposta à seca nas espécies de plantas dos Campos de Altitude;
(2) Determinar como a originalidade funcional encontra-se distribuída entre as espécies e estratégias;

(3) Avaliar a vulnerabilidade da comunidade à homogeneização funcional sob diferentes cenários de extinção de espécies.

Parte 3. O efeito das fontes alternativas de água:

(1) Verificar o quanto as espécies dos Campos de Altitude diferem na sua capacidade de absorção foliar de água;

(2) Avaliar quais características foliares (morfológicas, fisiológicas e anatômicas) são importantes para explicar essa variação interespecífica;

(3) Identificar potenciais associações entre a capacidade de absorção foliar de água e as estratégias ecológicas CSR;

(4) Validar a repelência e retenção foliar de água como características preditoras da capacidade das plantas realizarem absorção foliar de água;

(5) Testar se o tamanho da gota de água pode influenciar na mensuração das características de repelência e retenção foliar de água.

Figura 10 - Fotos das 76 espécies de plantas vasculares ocorrentes nos Campos de Altitude do Parque Nacional do Itatiaia (Rio de Janeiro, RJ, Brasil) e avaliadas neste estudo.

Legenda: família botânica e nome científico das 76 espécies avaliadas neste estudo: ALSTROEMERIACEAE: 1. *Alstroemeria foliosa* Mart. ex Schult. & Schult.f.; 2. *Alstroemeria isabelleana* Herb.; AMARYLLIDACEAE: 3. *Hippeastrum morelianum* Lem.; APIACEAE: 4. *Eryngium glaziovianum* Urb.; APOCYNACEAE: 5. *Oxypetalum glaziovii* (E. Fourn.) Fontella & Marquete; ASTERACEAE: 6. *Achyrocline satureioides* (Lam.) DC.; 7. *Baccharis altimontana* G. Heiden et al.; 8. *Baccharis brevifolia* DC.; 9. *Baccharis glaziovii* Baker; 10. *Baccharis grandimucronata* Malag.; 11. *Baccharis itatiaiae* Wawra; 12. *Baccharis parvidentata* Malag.; 13. *Baccharis pseudomyriochepala* Malag; 14. *Baccharis retusa* DC.; 15. *Baccharis stylosa* Gardner; 16. *Baccharis tarchonanthoides* DC.; 17. *Baccharis uncinella* DC.; 18. *Chaptalia runcinate* Kunth; 19. *Chionolaena capitate* (Baker) Freire; 20. *Gamochaeta purpurea* (L.) Cabrera; 21. *Graphistylis itatiaiae* (Dusén) B. Nord.; 22. *Grazielia gaudichaudiana* (DC) R.M. King & H. Rob; 23. *Hieracium commersonii* Monnier; 24. *Hypochaeris lutea* (Vell.) Britton; 25. *Leptostelma maximum* D.Don; 26. *Leptostelma tweediei* (Hook &Arn) DJN Hind & GL Nesom; 27. *Mikania camporum*

B.L. Rob.; 28. *Mikania glaziovii* Baker; 29. *Senecio adamantinus* Bong; 30. *Senecio nemoralis* Dusén; 31. *Senecio oleosus* Vell.; 32. *Stevia camporum* Baker; 33. *Trixis glaziovii* Baker; 34. *Symphyopappus reitzii* (Cabrera) R.M.King & H.Rob. BROMELIACEAE: 35. *Fernseea itatiaiae* (Wawra) Baker; CAMPANULACEAE: 36. *Lobelia camporum* Pohl; CARYOPHYLLACEAE: 37. *Cerastium dicrotrichum* Fenzl ex Rohrb.; CYPERACEAE: 38. *Machaerina ensifolia* (Boeckeler) T. Koyama; ERICACEAE: 39. *Agarista hispidula* (DC.) Hook. Ex. Nied.; 40. *Gaultheria serrata* (Vell.) Sleumer ex Kin.-Gouv.; 41. *Gaylussacia amoena* Cham.; 42. *Gaylussacia chamissonis* Meisn.; 43. *Gaylussacia fasciculata* Gardner; ERIOCAULACEAE: 44. *Paepalanthus itatiaiensis* Ruhland; ESCALLONIACEAE: 45. *Escallonia laevis* (Vell.) Sleumer; FABACEAE: 46. *Lupinus gilbertianus* C.P.Sm.; 47. *Mimosa itatiaiensis* Dusén; 48. *Mimosa monticola* Dusén.; GERANIACEAE: 49. *Geranium brasiliense* Progel; IRIDACEAE: 50. *Gelasine coerulea* (Vell.) Ravenna; 51. *Sisyrinchium alatum* Hook.; 52. *Sisyrinchium nidulare* (Hand. Mazz.) I.M. Johnst.; LAMIACEAE: 53. *Lepechinia speciosa* (A.St.Hil. ex Benth.) Epling; LENTIBULARIACEAE: 54. *Utricularia reniformis* A St.-Hill; MELASTOMATACEAE: 55. *Tibouchina sebastianopolitana* Cogn.; 56. *Leandra quinquedentata* (DC.) Cogn.; 57. *Pleroma hospita* (Schrank et Mart. ex DC.) Triana; MYRTACEAE: 58. *Myrceugenia alpigena* (DC.) Landrum; ONAGRACEAE: 59. *Fuchsia campos-portoi* Pilg. & Schulze-Menz; ORCHIDACEAE: 60. *Pelexia itatiayae* Schltr.; OROBANCHACEAE: 61. *Esterhazya splendida* J.C. Mikan; OXALIDACEAE: 62. *Oxalis confertissima* A.St.-Hil. PLANTAGINACEAE: 63. *Plantago australis* Lam.; 64. *Plantago guilleminiana* Decne POACEAE: 65. *Chascolytrum itatiaiae* (Ekman) Essi, Longhi-Wagner & Souza-Chies; 66. *Chusquea pinifolia* (Nees) Nees; 67. *Cortaderia modesta* (Döll.) Hack; POLYGALACEAE: 68. *Polygala brasiliensis* L.; 69. *Polygala campestris* Gardner; PRIMULACEAE: 70. *Myrsine gardneriana* A. DC.; PROTEACEAE: 71. *Roupala montana* Aubl.; ROSACEAE: 72. *Fragaria vesca* L.; RUBIACEAE: 73. *Coccocypselum condalia* Pers.; 74. *Coccocypselum cordifolium* Nees. & Mart.; 75. *Galium humile* Cham. &Schltdl.; SYMPLOCACEAE: 76. *Symplocos itatiaiae* Wawra.

Fonte: O autor, 2019.

1 FATORES QUE INFLUENCIAM A ESTABILIDADE DE VEGETAÇÕES CAMPESTRES EM RESPOSTA À SECA

> Everything should be as simple as it can be, but not simpler.
>
> *AlbertEinstein*

1.1 Deciphering ecological stability of grasslands productivity in response to experimental droughts

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1.1.1 Abstract

Rainfall manipulation experiments are essential for deciphering mechanisms leading to differential ecological stability across plant communities. However, the absence of standardized stability indices and common methodologies across studies has impaired the identification of general patterns of response. Here, we used meta-analysis tools and standardized drought indices to overcome the non-comparability across studies and then to evaluate the effects of experimental droughts on grassland above-ground biomass. We found that most grasslands were resilient (keeping biomass unchanged after drought) and exhibited a trade-off between low resistance (losing biomass during drought) and high recovery (producing new biomass after drought). Despite this general pattern, ecological stability varied across studies, not only because of differences in drought treatments (intensity, duration, frequency) or in prevailing climatic conditions (temperature, precipitation, seasonality), but may also because of intrinsic biotic and soil differences among grasslands. Drought effects, however, might be underestimated because half of the studies have failed on imposing a real drought event, and only a few have applied extreme droughts. In addition, studies have mostly focused on the immediate drought impact (resistance), neglecting the post-drought responses (recovery and resilience). We discussed those and other shortcomings of rainfall manipulation experiments and provided five main recommendations for ongoing and future studies.

Key-words: extreme climatic events; meta-analysis; rain-out shelters; resistance; recovery; resilience.

1.1.2 Introduction

Grasslands cover a large proportion of the land surface (Dixon et al. 2014) and their productivity is strongly controlled by precipitation (Knapp and Smit 2001). As the frequency, duration and intensity of droughts are predicted to increase (Sheffield and Wood 2008, Dai 2013) hundreds of rainfall manipulation experiments (Fig. 1) have been conducted to investigate the effects of shifted precipitation regimes on grassland above-ground biomass production. These experiments do not report consistent results (Stuart-Haëntjens et al. 2018, Wilcox et al. 2017, Wu et al. 2011), and the underlying mechanisms explaining differences in ecological stability in response to drought have not yet been identified (Hoover et al. 2018, Wilcox et al. 2017, Wu et al. 2011).

These inconsistencies may arise from lack of standardized experimental methodologies and protocols (Knapp et al. 2017, Smith et al. 2017), and absence of consistent definitions and standardized indices to assess ecological stability (Ingrisch and Bahn 2018). For instance, studies differ on the type of experimental drought imposed (Figs. 1a-c), and have often relied on indices of drought treatment intensity which are inappropriate for comparing sites with different precipitation regimes (Fig. 1; Hoover et al. 2018, Kreyling et al. 2017a, Vicca et al. 2012). Consequently, it is unknow whether the observed variation in stability responses might be attributed to intrinsic biological differences across systems or might merely reflect differences in the drought treatment or in the prevailing climatic conditions experienced by plants (Kreyling et al. 2017a, Smith et al. 2017).

Studies have also varied in their definition of stability and at least three distinct properties have been assessed: resistance, recovery and resilience (Ingrisch and Bahn 2018, Smith et al. 2017). In this context, resistance is defined as the grassland ability to keep its biomass unchanged during drought (Ingrisch and Bahn 2018). It measures the immediate impacts of drought on biomass, and thus a grassland is considered resistant if it does not lose biomass during the drought, i.e. the biomass in control and drought plots do not significantly differ (RT in Fig 1). Recovery is the grassland ability to produce new biomass after the drought (Ingrisch and Bahn 2018). It is obtained by comparing biomass in the drought plots immediately at the end of the drought and some time, usually one year, after drought cessation (post-drought). A grassland is considered able to recover, if the post-drought biomass is higher than the biomass during drought (RC in Fig 1). Finally, resilience is the system ability to maintain unchanged levels of biomass after drought (Ingrisch and Bahn 2018). A grassland is considered resilient if during the post-drought period the biomass between control and drought plots do not differ (RS in Fig 1). As different indices have been used to measure those properties, we are still uncertain about the trade-offs among them and their relative importance to underpin the overall grasslands ecological stability (Donohue et al. 2013).

Here, we searched for published studies reporting effects of experimental droughts on grasslands to: (1) identify which indices have been used to assess ecological stability and whether those indices provide comparable results or not; (2) evaluate the overall grasslands resistance, recovery and resilience in response to drought; (3) identify trade-offs between those properties; and (4) quantify the relative importance of drought experimental characteristics (intensity, duration and frequency), elevation, and prevailing climatic conditions (temperature, precipitation, rainfall seasonality) to explain the differential stability across grasslands.

1.1.3 Materials & Methods

1.1.3.1 Data search, inclusion criteria and meta-data extraction

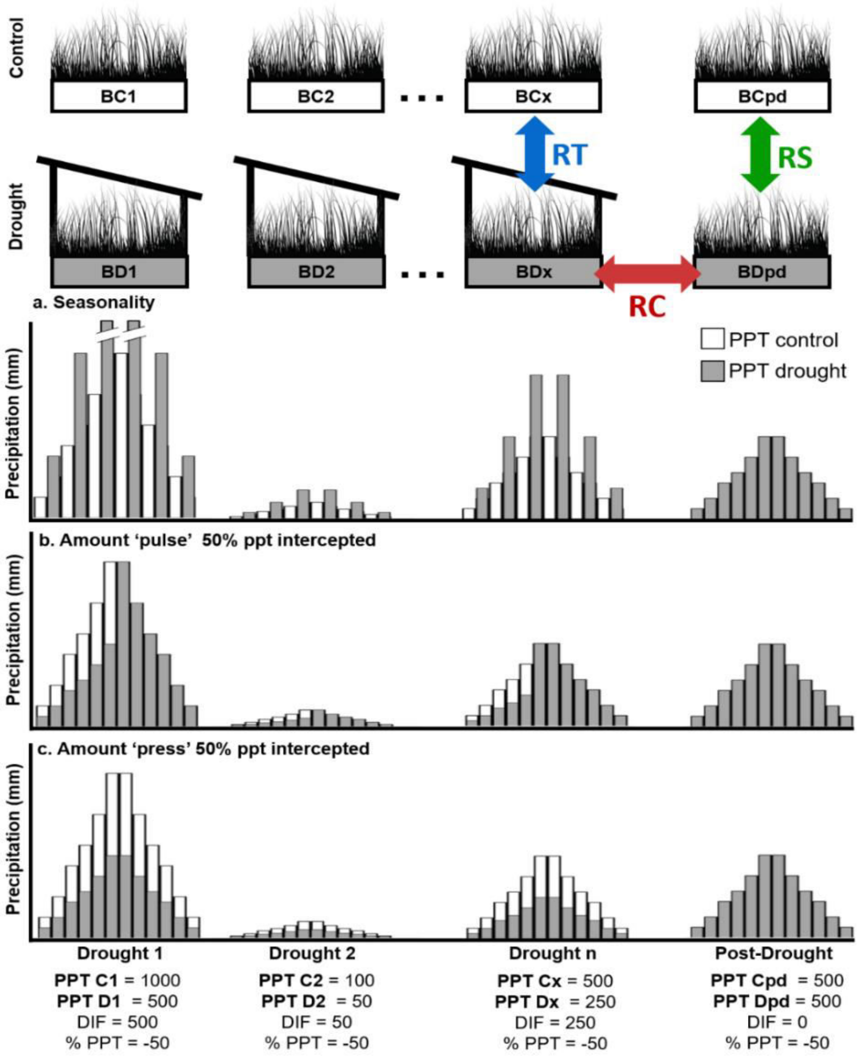
We searched for peer-reviewed scientific articles published before June 2018 that conducted rainfall manipulation experiments on grasslands across the globe. The search was conducted in two web databases: Google Scholar [search string: (in subject: grassland in title:(resilience OR resistance OR recovery OR stability OR vulnerability) AND (rain shelter OR rain exclusion OR rain manipulation OR drought OR precipitation) AND (plant OR tree OR grass OR vegetation)] and ISI Web of Science [search string: (grassland AND (drought OR rain* OR precipitation) AND (resistance OR resilience OR recovery OR stability OR vulnerability) AND (plant* OR tree OR grass OR shrub OR veget*)], and resulted in 278 relevant references. After cross-referencing, removal of duplicates, and application of a first set of inclusion criteria (Supplementary Note A), we retained a total of 127 articles (204 study cases) published during 1989 and 2018 (Supplementary Note A). From each study we extracted the following metadata: study location (coordinates, country and locality); elevation (m asl); mean annual temperature (MAT, °C); mean annual precipitation (MAP, mm); vegetation type (natural, seminatural or manipulated); shelter area (m²); shelter type (permanent - shelters covered vegetation all over the experimental drought period; or automatic - shelters were able to detect rainfall and only covered vegetation during rainfall events); control plot type (ambient - unsheltered control plots receiving ambient precipitation; or historic - sheltered control plots which are irrigated to receive rainfall amounts correspondent to historical precipitation recorded for the study area); drought type (amount - precipitation amount reduced by a fixed percentage; or seasonality - rainfall seasonality altered without significant changes in precipitation amount); drought duration (total number of days with shelters intercepting rainfall); drought frequency (number of sequential drought events) and drought magnitude (either reported as the percentage of rainfall intercepted by shelters; or as extremeness; that is, the probability of occurrence based on precipitation historical records, where a 100-year drought event is the one that has 1% chance of occurrence in any given year - Knapp et al. 2017); response variables measured on plants; and whether those studies reported indices of stability.

Subsequently, we computed stability indices and Hedges' g effect sizes (Borenstein et al. 2009) for a subset of 49 articles (101 study cases) which met a second set of inclusion criteria (Supplementary Note A). We decided to assess ecological stability only in terms of above-ground biomass, because it was the response variable most frequently reported (83 %; N = 170). In addition, we eliminated experiments altering only rainfall seasonality because their small sample size (N = 23) and their particular experimental design which precluded comparisons to amount drought types. Metadata was extracted directly from text or tables, or indirectly from figures using the Figure Calibration plugin in the Image J software, version 1.48. When elevation, MAT, and/or MAP were not provided in the original studies, they were derived using Geoplaner (http://www.geoplaner.com) and WorldClim (http://www.worldclim.org).

1.1.3.2 Stability indices and effect sizes

Firstly, we gathered all stability indices reported in the 127 articles. Secondly, we computed all the stability indices by using the biomass data provided in the subset of 101 study cases. Finally, we evaluated whether those indices provided comparable results or not.

Figure 1 - Overview of rainfall manipulative experiments.



Subtitle: experiments have used rain-out shelters to intercept rainfall in drought plots creating one or multiple sequential droughts (n=1, 2… x). Response variables, most frequently above-ground biomass, are measured on control (BCn) and drought plots (BDn) during the drought, and some time after drought cessation (post-drought: BCpd and BDpd). Biomass data can be used to estimate three stability properties: resistance (RT); recovery (RC); and resilience (RS). Precipitation (mm) for control (PPTCn) and drought plots (PPTDn) are shown for three droughts types: (a) seasonality: rainfall is repacked into larger events and longer dry intervals without changes in total amount; (b) amount 'pulse': rainfall amount is reduced by a fixed percentage (%PPT = -50 %) during shorter and interrupted periods; and (c) amount 'press': rainfall is reduced during longer and uninterrupted periods. Although the %PPT remains the same across drought period (-50 %), larger absolute differences between control and drought plots (DIF) are observed in wetter (Drought 1) than in drier years (Drought 2). Moreover, when comparing stability across distinct sites/grasslands, if the interannual variation in precipitation in one site is greater than that in another site, a drought of -50 % intensity is likely to have less effect on the former site. Therefore, %PPT is not a reliable index of drought intensity and it is not comparable across sites with distinct precipitation regime. BCn = biomass in control plots during drought; BDn = biomass in drought plots during drought; BCpd = biomass in control plots during post-drought; BDpd = biomass in drought plots during post-drought; RT = resistance; RC = recovery; RS = resilience; PPTCn = precipitation in control plots; PPTDn = precipitation in drought plots; %PPT = percentage of rainfall intercepted by rain-out shelters; DIF = absolute difference in precipitation between control and drought plots.

Source: The author, 2019.

To assess overall grasslands ecological stability in response to experimental droughts, instead of using those stability indices, we computed mean Hedges' g effect sizes for resistance, recovery and resilience (Borenstein et al. 2009). We used mean effect sizes because in this approach studies were weighted by their precision (more precise studies received larger weights), thus providing a more unbiased overall effect (Borenstein et al. 2009). Hedges' g effect sizes for resistance (N = 101) were obtained as the difference of above-ground biomass between drought and control plots during drought period; for recovery (N = 19), as the difference between post-drought and drought plots; and for resilience (N = 19), as the difference between drought and control plots during post-drought period. Those differences were then divided by the pooled standard deviation and weighted by sample size. Consequently, effect sizes represented the number of standard deviations by which the treatment differed from the control group (Borenstein et al. 2009), and negative/positive values indicated decreases/increases in above-ground biomass in treatment (drought) compared to control plots. Mean effect sizes for each stability property were estimated under random effect-models using restricted maximum likelihood estimation and Knapp and Hartung adjustment within the 'metafor' R package (Viechtbauer 2010). Lastly, linear regressions were used to test for potential trade-offs among stability properties. Assumptions of normality of residuals and homogeneity of variance of the linear regressions were checked graphically.

1.1.3.3 SPEI and rainfall seasonality computation

We calculate the SPEI, as a measure of experimental drought intensity, for each of the 101 study cases. We decided to used SPEI, instead of the percentage of rainfall intercepted because the former index accounts for the interannual precipitation variability and enables reliable comparisons across studies regardless the season, location or climate (Vicente-Serrano et al. 2010). For a given site, the SPEI represents the number of standard deviations by which the climatic water balance (precipitation minus potential evapotranspiration) differed from the monthly mean historical record, with negative/positive values indicating drier/wetter conditions as follow: extreme drought SPEI < -2.00; severe drought: -1.50 < SPEI

< -1.99; moderate drought: -1.00 < SPEI <-1.49; near normal conditions: -0.99 < SPEI < 0.99; moderate wet:1.00 < SPEI < 1.49; severe wet: 1.50 < SPEI <1.99; and extreme wet: SPEI > 2.00 (Vicente-Serrano et al. 2010).

To compute SPEI we firstly obtained, for each study location, the monthly precipitation and potential evapotranspiration data (Penman Montieth) from the TerraClimate database, which provides data of climatic water balance from 1958 to 2017 at a spatial resolution 2.5 arc minutes (~ 4 km; Abatzoglou et al. 2018). Secondly, the approximate monthly precipitation inputs for the control and drought plots during the whole drought period were determined based on the information provided by each study (i.e. percentage of rainfall intercepted and drought starting and ending dates) and then the precipitation values in the original climatic dataset were altered accordingly. For instance, for a study that would have applied an experimental drought by intercepting 50 % of rainfall from March to September 2005, we would simply divide by 2 the monthly precipitation values downloaded from TerraClimate for that specific period. Subsequently, we used the 'SPEI' R package (Vicente-Serrano et al. 2010) to calculate the one-month derivation of SPEI for the whole drought period. Finally, we estimated the drought intensity for each drought event by averaging SPEI values for the drought period. We also evaluated potential confounding effects of interannual precipitation variability over experiments by computing the SPEI for the control plots. In this case, we used the original values of monthly precipitation extracted from TerraClimate and checked if control plots were exposed to naturally drier/wetter conditions, either before (pre-drought: mean SPEI for 12 months before the starting drought date), during (drought: mean SPEI for the whole drought period) or after the experimental drought period (post-drought: mean SPEI for the period between the end of the drought and the post-drought biomass harvesting). SPEI for control plots were not computed for studies using historical control plots.

We recognize two main limitations of using SPEI as a measure of experimental drought intensity. Firstly, climatic water deficits do not necessarily lead to plant water deficits (Vicca et al. 2012). Even if rainfall manipulation experiments succeed in translating precipitation deficits to soil water deficits, they might fail to alter the potential evapotranspiration in a similar way that occurs during real drought events (Beier et al. 2012, Kreyling et al. 2017a). Secondly, there could be mismatches between the precipitation inputs extracted from TerraClimate and the actual precipitation received in the experimental sites.

However, as very few experiments provided the necessary data to calculate more meaningful metrics of drought intensity (Vicca et al. 2012), we believe our approach is justified.

The long-term precipitation data obtained from the TerraClimate database (1980-2017) was also used to compute the rainfall seasonality (Feng et al. 2013). Rainfall seasonality (S) ranges from 0 (no seasonality with rainfall uniformly distributed throughout the year) to 3.58 (maximum seasonality with rainfall concentrated in a single month), and was computed as (Feng et al. 2013): S = D* R/R max, where D is the relative entropy (i.e. a measure of the concentration rainfall around the wet season); R is the long-term mean annual rainfall for each site; and R max is the maximum mean annual rainfall in the dataset (R max=3,074 mm yr−1 in ALPFOR research station, Switzerland).

1.1.3.4 Effects of moderators

To verify whether grasslands varied in their stability in response to drought we used the Cochran's Q test, and we estimated the percentage of total variance that could be attributed to between-studies rather than to sampling error (I^2) (Borenstein et al. 2009). Significant differences from Cochran's Q-tests ($p < 0.05$) and high percentages of between-studies heterogeneity (usually $I^2 > 50$ %) indicate that grasslands significantly varied in their stability (Borenstein et al. 2009). Subsequently, to quantify the relative importance of drought experimental features (duration, frequency and intensity- SPEI), prevailing climatic conditions (MAT and MAP, rainfall seasonality) and elevation to explain the differential stability across grasslands we used multi-model inference (Burnham and Anderson 2002). In this analysis all possible unique models involving the above set of moderators were fit using random-effect meta-regression linear models, and ranked according to the second-order Akaike information criterion (AICc). For each moderator, we computed the model-averaged estimate and relative importance. Relative importance was obtained by summing the Akaike weights of all models that included the moderator of interest. Values of relative importance greater than 0.8 indicated that the moderator was important to explain the variation in the stability properties (Burnham and Anderson 2002). Separated models were constructed for resistance, recovery and resilience using functions from the 'glmulti' (Calcagno and Mazancourt 2010) and 'metafor' R packages (Viechtbauer 2010). Additionally, we fit simple meta-regression models to evaluate the effect of moderators related to experimental characteristics (vegetation type; shelter area; shelter type and control plot type).

1.1.3.5 Sensitivity Analysis

We performed sensitivity analysis, using the ‘metafor’ R package, to test for the effect of outliers, publication bias and non-independence problems (Viechtbauer 2010). To deal with non-independence in studies performed with more than two levels of species biodiversity, we restricted our analysis to the most diverse treatment; that is, the treatment with the highest number of species. When a single study reported results from experiments conducted in different locations, each locality was treated as an independent study case. Subsequently, we used hierarchical models to test for non-independence of studies conducted at the same locality. Finally, in studies reporting sequential drought events, stability indices and effect sizes were computed using only the biomass data for the last drought event (final). To evaluate the extent to which our results were robust to this decision, we also computed the effect sizes using biomass data averaged across all drought events (averaged) and presented their results in the Supplementary Note B.

1.1.4 Results

1.1.4.1 Metadata

Rainfall manipulation experiments were conducted in 22 countries and 116 localities (Fig. 2), either in natural (40 %; N = 82), seminatural (39 %; N = 80) or manipulated grasslands (20 %; N = 42). Most of the studies (95 %; N = 110) were performed at mid-to-high latitudes (30–60°) in the northern hemisphere. Climatically, experiments were carried out in locations with mean annual temperature (MAT) ranging from 0.1° to 22.7 °C (median = 8.5 °C) while elevation (m asl.) ranged from 5 to 3,570 m (median = 612 m). Mean annual precipitation (MAP) ranged from 163 to 2,050 mm (median = 771 mm). We found that, for most of the sites, rainfall is well distributed throughout the year (median = 0.02, range 0.0027 – 0.1969). Droughts were imposed using shelters with different sizes (median = 9 m², range: 0.5 to 900 m²), either automatic (9 %; N = 19) or permanent (91 %; N = 185). Most studies reduced total rainfall (90 %; N = 184) rather than altered rainfall seasonality (6 %; N = 12) or both (4 %; N = 8). Drought duration ranged from 17 to 2,310 days, with most studies being short-term experiments (< one year) and only 9% of them (N = 4) lasting more than ten years. Similarly, most studies imposed a single drought event (46 %; N = 95), with a maximum of 15 sequential droughts (median = 2).

In most of the studies (73 %; N = 149) drought intensity was measured as the percentage of rainfall intercepted by shelters, which ranged from 8 to 80 % reduction in annual precipitation. However, some authors defined experimental droughts in terms of their statistical extremeness (15 %; N = 30), which ranged from 1 to 1000-year. Historic control plots were used only in a few experiments (16 %; N = 32), in contrast to ambient controls that were used in 84 % (N = 172) of the studies. When drought intensity was measured using SPEI, we found that 28 % of the studies (N = 31) imposed moderate droughts, while 14 % (N = 16) created severe droughts and only 8% (N = 9) conducted extreme drought events. Surprisingly, in 50 % of the studies (N = 55) the ‘drought’ treatment actually did not experience a deficit in water balance, as the SPEI values were still in the range of near normal conditions. We found that control plots - either before (pre-drought), during (drought) and after (post-drought) the experimental drought period - were usually exposed to near normal conditions, except in two study cases, where control plots were subjected to moderately wet conditions.

1.1.4.2 Stability indices

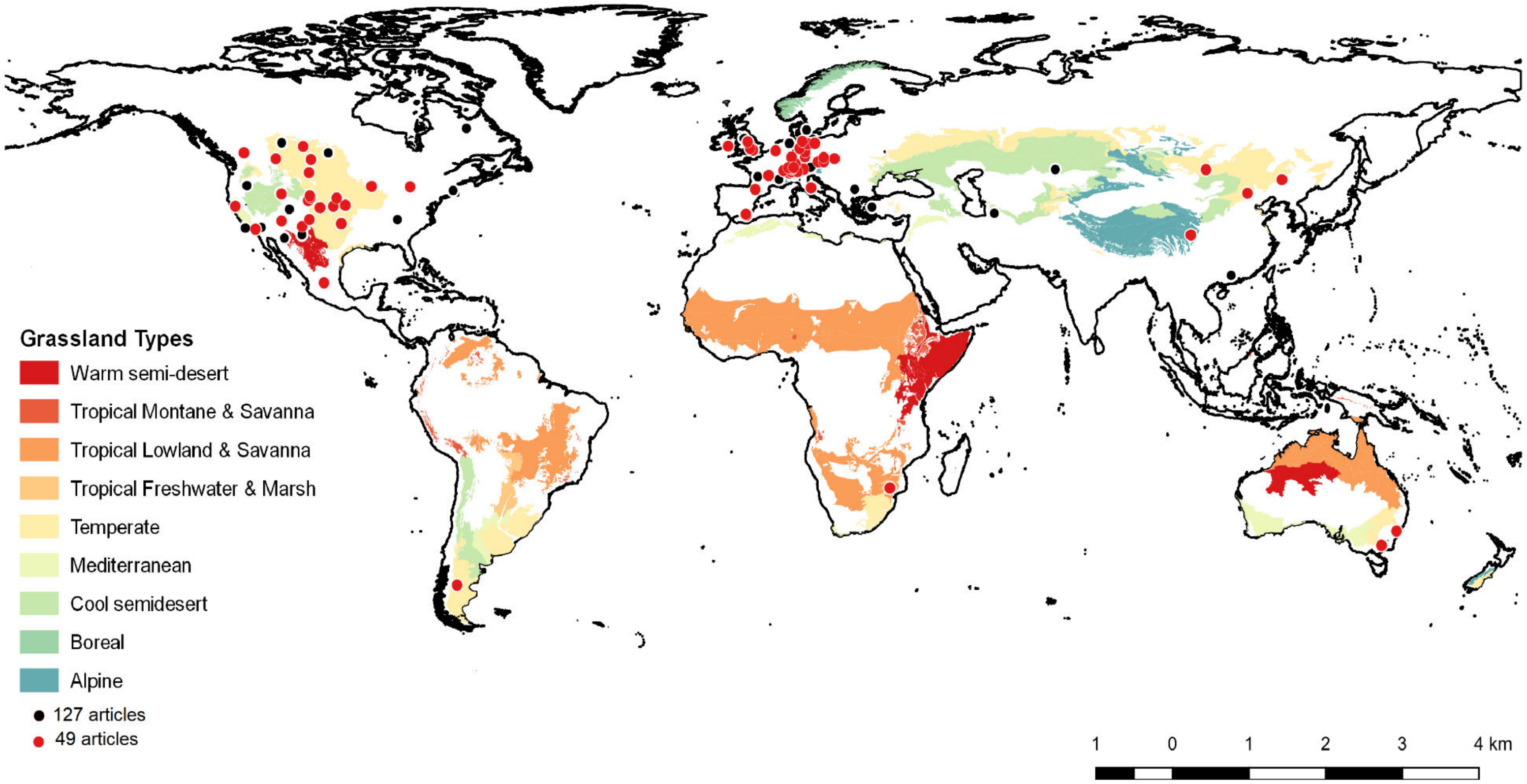
Only 13 % (N = 17) of the studies applied stability indices to assess grassland resistance, recovery and/or resilience in response to drought. We grouped those indices in six groups (Table 1), according to the type of stability property assessed (resistance – RT; recovery – RC; resilience – RS; or relative resilience – RRS) and the way the stability was quantified (group 1 – raw difference; group 2 – simple ratio; group 3 and 4 – compounded ratio; group 5 – natural logarithm ratio; group 6 – standardized ratio).

Although none of the selected studies have measured recovery as raw difference (RC1) or compounded ratio (RC3 and RC4); or resilience as compounded ratio (RS3) we decided to add those indices in our study to enable a full comparison across the six indices groups. Thus, we obtained 19 stability indices in total. When the 101 grasslands where ordered according to their values on recovery, resistance, and resilience, different rankings were obtained depending on the indices considered. Therefore, results from studies using different groups of stability indices were not comparable (Supplementary Note C).

1.1.4.3 Overall grasslands stability in response to drought

Resistance assumed significantly negative values (Fig. 3a), thus indicating that above-ground biomass was strongly reduced during drought. In contrast, recovery was significantly positive (Fig. 3b), indicating that grasslands were able to produce new biomass after drought alleviation. The biomass produced after drought was in general sufficient to compensate for the biomass lost during drought, thus grasslands exhibited nearly full resilience (i.e. resilience was not significantly different from zero; Fig. 3c). Although we argue that this result might be overestimated, because few studies have subjected grasslands to severe or extreme drought events.

Figure 2 - Global map displaying site location of rainfall manipulation experiments conducted in grasslands.



Subtitle: black dots indicate the location of 204 study cases (extracted from 127 articles that met the first set of inclusion criteria), while red dots indicate the location for 101 study cases (extracted from 49 articles that met the second set of inclusion criteria) that were used for quantitative analysis (inclusion criteria are listed in Supplementary Note A). Grasslands types and distributions were obtained from Dixon et al. 2014.

Source: The author, 2019.

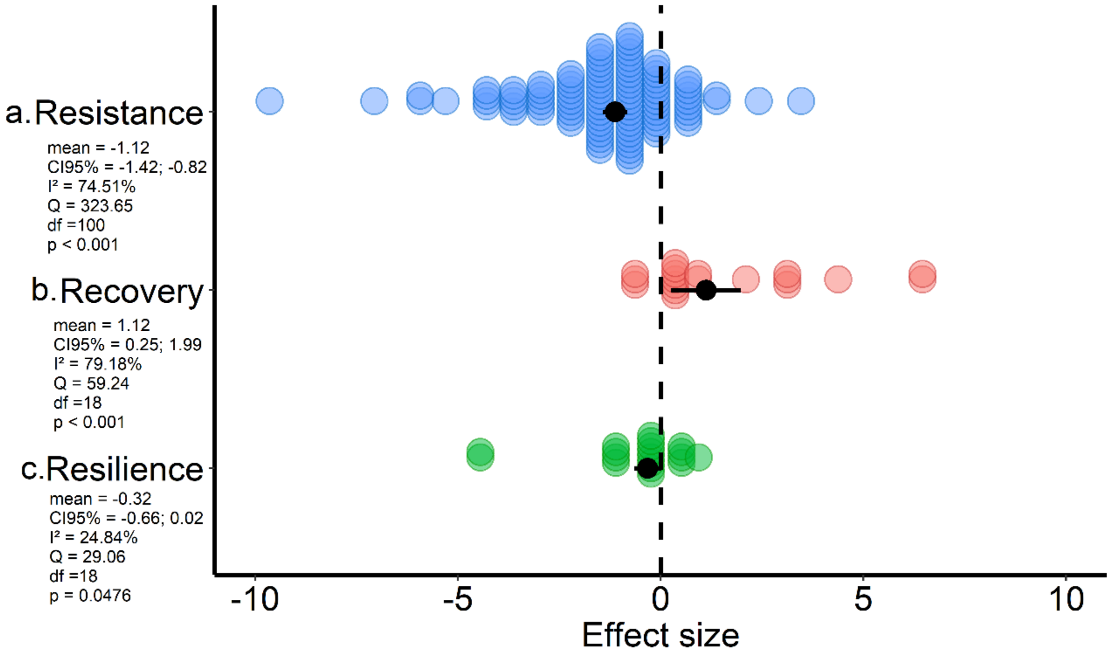
Table 1 - Stability indices used to assess resistance (RT), recovery (RC), resilience (RS) and relative resilience (RRS) of grasslands in response to experimental droughts.

Group	Resistance (RT)	Recovery (RC)	Resilience (RS)	Relativeresilience (RRS)
1	$RT1 = BD – BC$ [18, 23, 25, 38, 31]	$RC1 = BD_{pd} – BD$*	$RS1 = BD_{pd} – BC_{pd}$[28]	$RRS1 = (BD_{pd} / BC_{pd}) - (BD / BC)$[21]
2	$RT2 = BD/BC$[20-22, 24, 28, 31]	$RC2 = BD_{pd}/BD$[18]	$RS2 = BD_{pd}/ BC_{pd}$[18, 20-25, 28]	$RRS2 = (BC_{pd}/(BD_{pd} - BC_{pd}))/(BC/ (BD – BC))$ [29]
3	$RT3 = (BD - BC)/ BC$[19, 31-32]	$RC3 = (BD_{pd} - BD)/ BD$*	$RS3 = (BD_{pd} - BC_{pd})/BC_{pd}$ *	
4	$RT4 = BC/ (BD – BC)$ [29]	$RC4 = BD/ (BD_{pd} – BD)$*	$RS4 = BC_{pd}/(BD_{pd} - BC_{pd})$ [29]	
5	$RT5 = \ln (BD/BC)$ [17, 18, 20, 27, 32]	$RC5 = \ln (BD_{pd} / BD)$ [18]	$RS5 = \ln (BD_{pd} / BC_{pd})$ [25]	
6	$RT6 = \frac{(BD/BC)/ (PPT_D/PPT_C)}{BC/PPT_C}$[26]	$RC6 = \frac{(\mathrm{BDpd}/\mathrm{BD})/ (PPT_{PD}/PPT_D)}{BC/PPT_C}$[28]		

Subtitle: stability indices classes: group 1 – raw difference; group 2 – simple ratio; group 3 and 4 – compounded ratio; group 5 – natural logarithm ratio; group 6 – standardized ratio; Biomass in control (BC) and drought (BD) plots during the drought period; biomass in control (BCpd) and drought (BDpd) plots during the post-drought period; precipitation in control (PPTC) and drought plots (PPTD) during the drought period and in both plots during the post-drought period (PPTPD). Numbers between brackets indicate references reporting each index: 1. Byrne et al. 2017; 2. Carter and Blair 2012; 3. Hoekstra et al. 2015; 4. Hofer et al. 2016; 5. Ingrisch et al. 2018; 6. Kreyling et al. 2017b; 7. Lanta et al. 2012; 8. Mariotte et al. 2013; 9. Pfisterer and Schmid 2002; 10. Shinoda et al. 2010; 11. Stampfli et al. 2018; 12. Vogel et al. 2012; 13. Wagg et al. 2017; 14. Wang et al. 2007; 15. Wang et al. 2014; 16. Yahdjian and Sala 2006; 17. Dormann et al 2017 * indices not reported in any of the 127 references used in the meta-analysis, but derived here to fill all indices groups.

Source: The author, 2019.

Figure 3 - Effects of experimental droughts on grasslandsabove-ground biomass.



Subtitle: Hedges'g effect sizes for resistance (**a**), recovery (**b**) and resilience (**c**) of grasslands above-ground biomass (N = 101) in response to experimental droughts. In studies reporting sequential drought events effect sizes were computed using biomass data only for the last experimental drought. Negative/positive values indicate decreases/increases in biomass in treatment plots compared to control plots. Black dots/lines indicate mean effect sizes and its 95% confidence interval (CI). Q-statistics, degree of freedom (df); p-value and the proportion of the observed variance that reflects true differences among studies (I^2) testing for between-studies heterogeneity.

Source: The author, 2019.

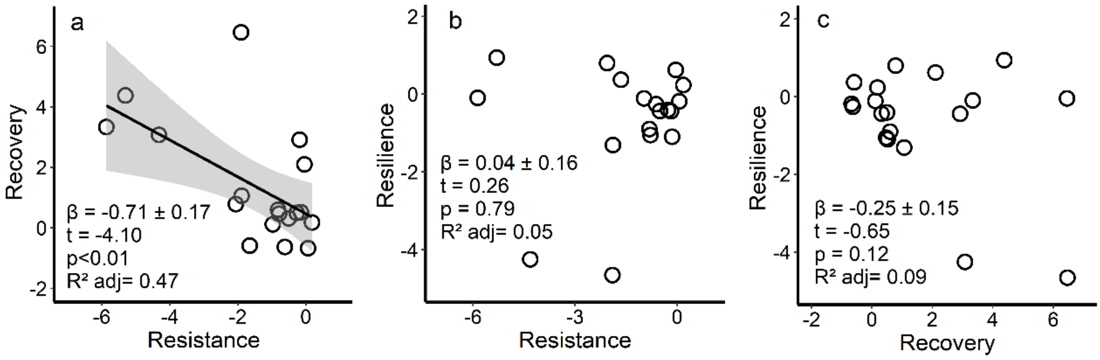
There was also a trade-off between recovery and resistance (Fig. 4a). However, no predictable relationships were found between the others stability properties (Fig. 4 b-c).

1.1.4.4 Differential stability across grasslands

We found large variation in resistance, recovery and resilience among grasslands (Fig. 3). However, drought characteristics (duration, frequency and intensity -SPEI), elevation and climatic conditions (MAT, MAP and rainfall seasonality) were not important to explain the variability in resistance and recovery (Fig.5 a-b). In contrast, variability in resilience was explained by drought duration (Fig. 5c), with longer droughts resulting in lower resilience

(Table 3 in Supplementary Note B). Results for simple meta-regressions testing the effect of moderators related to other experimental characteristics (vegetation type; shelter area; shelter type and control plot type) are shown in Table S1.

Figure 4 - Simple linear regressions testing for potential trade-offs among stability properties.



Subtitle: resistance, recovery and resilience were computed as Hedges'g effect sizes measuring the effects of experimental droughts on above-ground biomass of 101 grasslands. In studies reporting sequential drought events effect sizes were computed using biomass data only for the last experimental drought.

Source: The author, 2019.

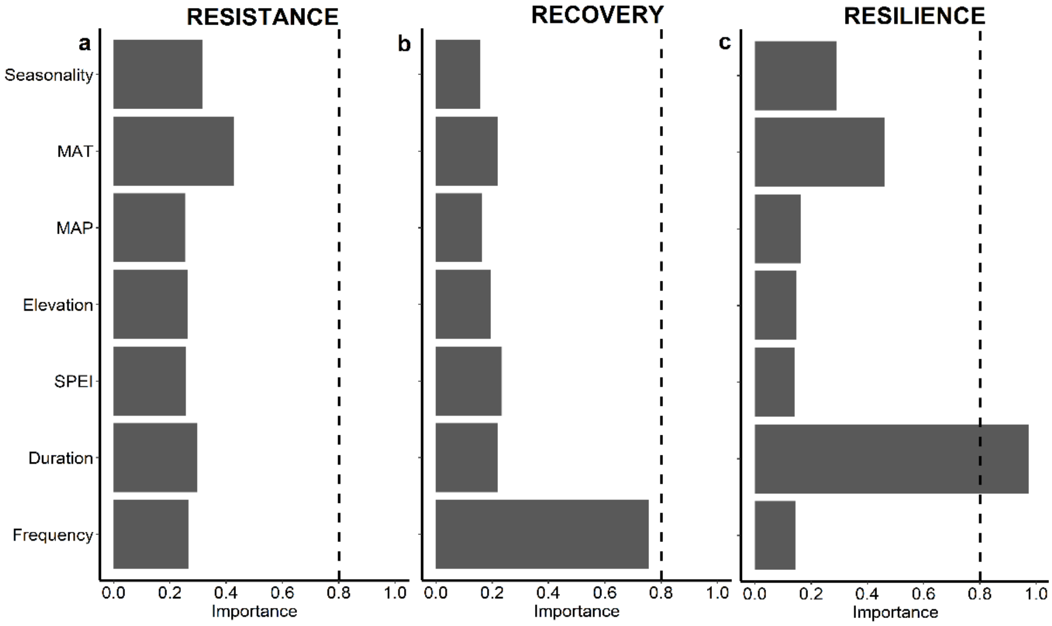
1.1.4.5 Sensitivity analysis

Our results were robust to the influence of outliers and non-independence effects. Nonetheless, evidence of publication bias was detected for resilience (Supplementary Note B).

1.1.5 Discussion

This study provides key insights into how grasslands respond to experimental droughts and also highlights the striking lack of consistency on methodological and analytical approaches to study the ecological stability of grasslands to drought.

Figure 5 - Relative importance of seven moderators to explain variability in grasslands stability.



Subtitle: model-averaged importance of seven moderators explaining grasslands resistance (a), recovery (b) and resilience (c) in terms of above-ground biomass in response to experimental droughts. Moderators: rainfall seasonality (Seasonality, dimensionless); mean annual temperature (MAT, ºC); mean annual precipitation (MAP, mm); elevation (m asl); standardized precipitation evapotranspiration index (SPEI) as a measure of drought intensity; drought duration (days); and drought frequency (number of sequential drought events). The vertical dashed line drawn at 0.80 can be used as a cut-off to identify important moderators. In studies reporting sequential drought events effect sizes were computed using biomass data only for the last experimental drought.

Source: The author, 2019.

We found that grasslands above-ground biomass was, on average, resilient to experimental droughts (Fig. 3). Grasslands ecological stability was achieved more via recovery than via resistance (Fig. 3), thus leading to a trade-off between these properties (Fig.4a). This trade-off is consistent with previous studies on supporting theoretical assumptions that resistance and recovery might be considered as two alternate strategies to achieve ecological stability (Donohue et al. 2013, Ruppert et al. 2015). It has been suggested that those strategies could be predicted by the life and evolutionary histories of resident plant species (Grime 2001, Grime and Pierce 2012, Reich 2014). Therefore, plant communities dominated by fast-growing short-lived species (acquisitive resource-use strategy) would be expected to show low resistance, as they lack traits to sustain biomass production under water stress. However, they would show high recovery. After drought alleviation, their high investment in seed production and fast-growth rates would support a shortly return to the non-drought biomass levels (Grime 2001, Grime and Pierce 2012, Reich 2014). An opposite response would be predicted for communities dominated by slow-growing and long-lived species (i.e. conservative resource-use strategy) (Grime 2001, Grime and Pierce 2012, Reich 2014). Once grasslands are mostly dominated by herbaceous species with an acquisitive strategy, we would indeed expect an overall resilience mainly driven by recovery than by resistance (Stuart-Haëntjens et al. 2018).

Despite this general pattern, grasslands significantly differed in their degree of resistance, recovery and resilience to drought (Fig. 3). However, none of the seven moderators we tested (drought duration, frequency and intensity, MAT, MAP, rainfall seasonality and elevation) were important to explain the variability in resistance and recovery across grasslands (Fig. 5 a-b). Therefore, the differential ecological stability did not merely reflect differences in the drought treatments imposed or in the prevailing climatic conditions, but they could be related to intrinsic biological differences across grasslands.

In fact, considerable evidence from individual studies suggests that species diversity (Kreyling et al. 2017b, Pfisterer and Schmid 2002, Vogel et al. 2012, Wagg et al. 2017); functional diversity (grass, legumes and forbs) (Byrne et al. 2017, Hofer et al. 2016, Stampfli et al. 2018); and plant life history traits (annual versus perennial) (Hoeppner and Dukes 2012, Wang et al. 2014) can significantly influence grasslands ecological stability in response to drought. Moreover, in a meta-analysis assessing the effects of natural droughts on productivity, it was found that variation in resistance and recovery across dryland communities was largely explained by plant life history, with perennial plants showing high resistance but low recovery, and annual plants exhibiting the opposite pattern (Ruppert et al. 2105). Soil characteristics - such as texture, depth and soil water content at field capacity - could also be important to explain the variation in resistance and recovery (Vicca et al. 2012, Wilcox et al. 2017). To date, most of the studies have not reported soil characteristics, species and functional diversity at plot-level, nor provided the life history traits (or any other traits related to the acquisitive-conservative strategies) for both dominant and subordinate plant species. Therefore, we strongly recommend future studies to provide such information, so that further quantitative analysis could be able to simultaneously assess the relative importance of both abiotic and biotic moderators to explain the differential stability across grasslands in response to experimental droughts.

In contrast, we found that drought duration was important to explain variability in resilience (Fig. 5c), with longer droughts resulting in decreased grassland resilience. Longer droughts could reduce resilience either by decreasing grasslands ability to recover from droughts (e.g. by causing depletion of seed bank and storage resources needed for re-establishment and resprouting of the drought-sensitive species) or their ability to resist to droughts (e.g. by surpassing thresholds of tolerance and causing widespread mortality of the drought-tolerant species) (Estiarte et al. 2106, Grime and Pierce 2012, Ruppert et al. 2015). Under future climatic regimes where droughts are expected to be longer, and also more frequent and intense, there might be a gradual decline in overall grasslands biomass. However, the evidence of publication bias detected for resilience indicates that these results must be interpreted with caution.

To further improve our mechanistic understanding of differential stability across grasslands and our ability to manage them to ensure a stable productivity in a drier world, we provide the following recommendations for future studies. (1) Standardize ecological stability indices: we found that different stability indices might provide largely divergent results (Supplementary Note C); thus, reinforcing the need for standardization across studies (Ingrisch and Bahn 2018, Smith et al. 2017). (2) Report basic information necessary to compute ecological stability indices and to assess the effect of moderators: we show that each stability index has its pros and cons (Supplementary Note C), thus regardless of the metric eventually selected as standard, we recommend studies to fully report biomass and precipitation data, which could be further used to recalculate stability using any of the indices. Moreover, studies should report sufficient plot-level information (such as plant functional diversity and soil characteristics) for further assessment of moderator effects. Previous publications have provided excellent guidance about which information studies should report (Beier et al. 2012, Gerstner et al. 2017, Smith et al. 2014). (3) Evaluate the three ecological stability properties simultaneously: we found that the majority of studies have only assessed grasslands resistance; thus, possibly overestimating the negative effects of droughts over grasslands production and also impairing a better assessment of the trade-offs between stability properties (Donohue et al. 2013). We then recommend the evaluation of both drought (resistance) and post-drought system responses (recovery and resilience). (4) Impose multiple and more extreme drought treatments: we showed that many studies have actually failed to impose experimental droughts and have assessed drought intensity by using inappropriate metrics (e.g. percentage of rainfall intercepted). Future experiments must consider local historical precipitation records (Vicca et al. 2012, Lemoine et al. 2016) and must use more meaningful metrics to determine the magnitude of the drought treatment (Hoover et al. 2018, Kreyling et al. 2017a, Vicca et al. 2012). Whenever possible, they should also impose multiple drought levels, including more extreme droughts, in order to better identify thresholds in grasslands response (Knapp et al. 2018). (5) Evaluate ecological stability of tropical grasslands: although tropical grasslands contribute to approximately 38% of world's grassland area (Dixon et al. 2014), most of the experiments were conducted in the northern hemisphere (Fig. 2). Thus, caution is required in extrapolating our results to the tropics, and future studies should expand the geographic extent of drought experiments to those understudied areas (Beier et al. 2012, Hoover et al. 2018). Collaborative initiatives, such as the Drought-Net (Knapp et al. 2017, Smith et al. 2017), could help on this and also could lead to the standardization of methodological approaches across studies; thus, facilitating further assessments of how and why plant communities differ in their ecological stability in response to drought.

Despite the focus of our study upon grasslands, we argue that the main shortcomings listed here and improvements suggested should guide future experimental studies evaluating effects of drought in different ecosystems.

1.1.6 References

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1.1.7Acknowledgements

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1.1.8Additional Information

Supplementary Note A: List of inclusion criteria and references included in the meta-analysis.
Supplementary Note B: Results of sensitivity analysis testing the influence of outliers, publication bias and non-independence.
Supplementary Note C: Comparisons among stability indices used to assess grasslands above-ground biomass resistance, recovery and resilience in response to experimental droughts.
Table S1: Results of simple meta-regressions testing the effects of moderators related to experimental characteristics (vegetation type; shelter area; shelter type; and control plot type) on the Hedges’ g effect sizes for grasslands resistance (RT), recovery (RC) and resilience (RS) in response to experimental droughts.

Supplementary Note A: List of inclusion criteria and references included in the meta-analysis.

First set of inclusion criteria:

[1] Experiments were conducted in the field (not greenhouses, growth chambers or individual pots) in natural, seminatural and/or manipulated plant communities (e.g. seeding in the field, transplantation of intact monoliths, mesocosms) which were composed by at least two species (not monocultures);

[2] Experiments were conducted in grasslands (i.e. herbs comprising more than 50 % of plant cover);

[3] Precipitation amount was decreased and/or rainfall seasonality was experimentally altered via rain-out shelters;

[4] Response variables were measured in adult vascular plants (not seedlings) on both drought (treatment) and non-drought (control) plots.

Second set of inclusion criteria:

[1] Precipitation amount was decreased in drought plots;

[2] Studies provided sample sizes (n) and above-ground biomass mean ± standard deviation (or standard error or confidence interval) for both control and drought plots;

[3] Studies informed starting and ending dates for the drought period and the percentage of rainfall intercepted by rain-out shelters.

List of papers that attended the first set of inclusion criteria. References in bold also attended the second set of inclusion criteria and were then used to compute stability indices and effect sizes. The other references did not meet the second set of inclusion criteria, and the number after each reference indicates which of the second set of inclusion criteria was not met. Asterisk indicates references not included because, although they met all inclusion criteria, they presented data duplicated with those provided by other articles already included in the meta-analysis.

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Supplementary Note B: Results of sensitivity analysis testing the influence of outliers, publication bias and non-independence.

Influence of outliers

To check for the effects of outliers, we firstly used the 'influence' function from the 'metafor' R package (Viechtbauer 2010) to identify influential studies. No influential points were detected for resistance (final), recovery (averaged) and resilience (both final and averaged). One influential study was detected for resistance (averaged) (de Boeck et al. 2016) and another for recovery (final) (Hoover et al. 2006).

Subsequently, we used the 'leave1out' function from the 'metafor' R package to assess whether the exclusion of those influential studies could change the overall results. We compared the estimates, p-values and second-order Akaike information criteria (AICc) obtained with and without the presence of the influential points (Table 1) and no relevant differences were observed, indicating that our results were robust for effects of outliers.

Table 1 - Checking the influence of outliers on estimation of mean effect sizes for grasslands stability in response to experimental droughts.

Effectsize	**Withinfluentialstudy**			**Withoutinfluentialstudy**		
	Estimate ± se	**p-value**	**I^2**	**Estimate ± se**	**p-value**	**I^2**
RT averaged	0.3965	<0.01	68.21	0.4107	<0.01	65.90
RC final	0.3966	<0.01	68.19	0.3966	<0.01	68.19

Subtitle: estimates ± standard error, p-value and percentage of total variance that could be attributed to between-studies rather than to sampling error (I^2) between models with and without the presence of influential studies. RT averaged: Hedges' g effect sizes for grasslands resistance to drought computed using above-ground biomass data (N = 106) averaged across all drought events and RC final: Hedges' g effect sizes for grasslands recovery from drought computed using above-ground biomass data (N = 101) only for the last drought event.

Source: The author, 2019.

Publication bias

To assess publication bias we used the Rosenthal's fail-safe number (N) which compute how many missing studies we would need to retrieve and incorporate in the meta-analysis before the p-value became non-significant (Rosenthal 1979). If N was greater than 5k + 10, where k is the number of studies already in the meta-analysis, the results can be considered robust. N was calculated using the ‘fsn’ function from the ‘metafor’ R package. Results for resistance (RT final: N = 8, 542 > 5k + 10 = 510; RT averaged: N = 7, 161 > 5k + 10 = 535) and recovery (RC final: N = 215 > 5k + 10 =110; RC averaged: N = 171 > 5k + 10 = 95) where robust, but for resilience they were not (RS final: N = 28 < 5k + 10 = 110; RS averaged: N = 21 > 5k + 10 = 95).

Non-independence

We have to deal with three distinct types of non-independence: multiple levels of species biodiversity; multiple locations and multiple sequential drought events.

Multiple levels of species diversity: to deal with non-independence in studies performed with more than two levels of species biodiversity, we restricted our analysis to the most diverse treatment; that is, the treatment with the highest number of species.

Multiple locations: when a single study reported results from experiments conducted in different locations, each locality was treated as an independent study case. Subsequently, we used hierarchical models to test for non-independence of studies conducted at the same locality. To account for this, study location was designated as a random effect within the mixed-effects model using the ‘rma.mv’ function from the ‘metafor’ R package. We compared models with (model 1) and without (model 2) accounting for non-independence and no large differences were found on estimates, p-values and AICc obtained for resistance, recovery and resilience, hence suggesting that our results were robust for non-independence related to multiple locations (Table 2).

Multiple sequential drought events: in studies reporting sequential drought events, stability indices and effect sizes were computed using only the biomass data for the last drought event (final). To evaluate the extent to which our results were robust to this decision, we also computed the effect sizes using biomass data averaged across all drought events (averaged). We presented the results for effect sizes final in the main text (49 articles; 101 study cases for RT; 19 study cases for RC and RS), while here we presented the results for averaged effect sizes (54 articles; 106 study cases for RT; 16 study cases for RC and RS).

When effect sizes were averaged across all grasslands we found that grasslands were not resistant (Fig. 1a), but were able to recover from drought (Fig. 1b) and achieved near fully resilience (Fig. 1c). Results were then similar to those found for effect sizes final (see Fig.3 in the main text). Regarding the trade-offs between stability properties, similarly what we found for effect sizes final (see Fig. 4a,c in the main text), we also observed a trade-off between recovery and resistance (Fig. 2a) and no predictable relationships between resilience and recovery (Fig. 2c). However, we found here a positive relationship between resilience and resistance (Fig.2b), which had not been detected when using effect sizes final (see Fig. 4b in the main text).

Table 2 - Checking for non-independence of studies conducted at the same locality.

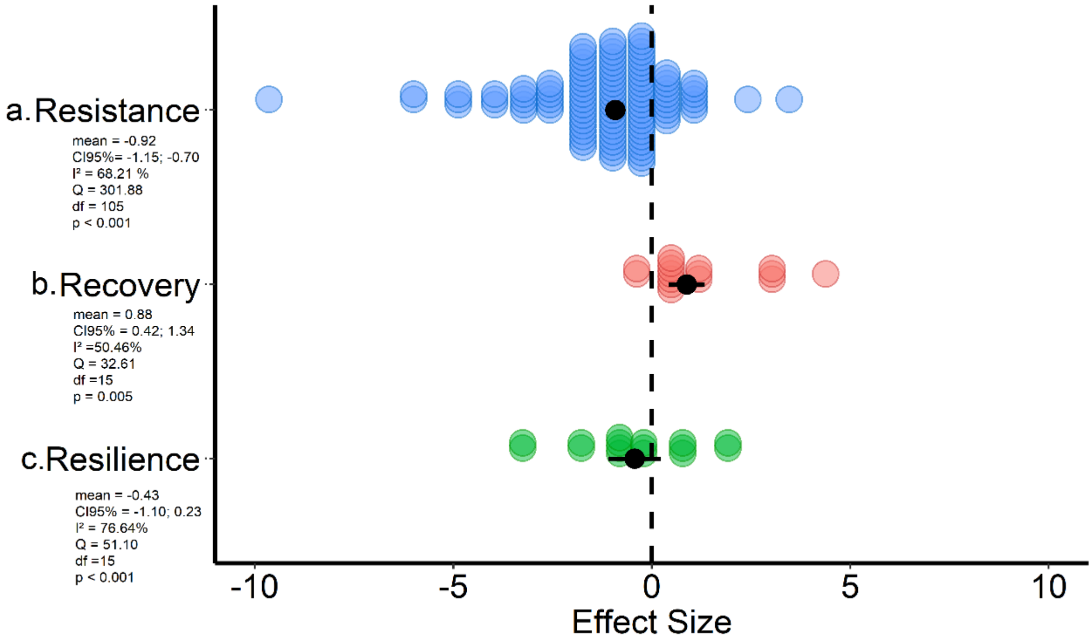
Effectsize	**Model 1** **Estimate ± se**	**p-value**	**AICc**	**Model 2** **Estimate ± se**	**p-value**	**AICc**
RT final	-1.19 ± 0.21	<.0001	407.98	-1.14 ± 0.15	<.0001	375.41
RT averaged	-1.02 ± 0.18	<.0001	374.22	-0.94 ± 0.12	<.0001	370.15
RC final	0.98 ± 0.43	0.0244	82.62	1.12 ± 0.41	0.0148	78.99
RC averaged	1.18 ± 0.42	0.0054	51.95	0.88 ± 0.23	0.0002	52.56
RS final	-0.21 ± 0.20	0.3003	52.07	-0.32 ± 0.17	0.0647	53.97
RS averaged	-0.56 ± 0.52	0.2845	61.29	-0.43 ± 0.34	0.2030	59.09

Subtitle: estimates ± standard error, p-value and second-order Akaike Information Criteria (AICc) between models with (model 1) and without (model 2) accounting for non-independence. Hedges'g effect sizes were computed for grasslands resistance (RT), recovery (RC) and resilience (RS) to experimental drought in terms of above-ground biomass. In studies reporting sequential drought events we computed effect sizes either considering only the biomass for the last drought event (final; N = 101) or the biomass averaged across all droughts (averaged; N = 106).

Source: The author, 2019.

We tested for heterogeneity in Hedge's g effect sizes across studies and found high (I^2 range: 50.5 - 76.7 %) and significant levels of between-studies heterogeneity for all the three stability properties (Fig. 1). However, according to our results for multi-model inferenced, none of the seven moderators tested – rainfall seasonality, seasonality (dimensionless); mean annual temperature, MAT (ºC); mean annual precipitation, MAP (mm); elevation (masl); averaged standardized precipitation evapotranspiration index, SPEI averaged (dimensionless); drought duration (days); and drought frequency (number of drought events) - were important to explain the variability in resistance, recovery and resilience across grasslands (relative importance < 0.8; Fig. 3 a-c). Results for simple meta-regressions testing the effect of moderators related to experimental features, both for effect sizes final and averaged, were shown in Supplementary Table S1. Finally, our approach to define drought intensity based on SPEI values slightly differed from the one proposed by McKee et al (1993), while they defined drought intensity as the sum of SPEI values for all the months within a drought event; in this study we averaged the SPEI values. In the Table 3 we compared the results of multi-model inference using either SPEI values averaged (SPEI averaged) or summed (SPEI sum).

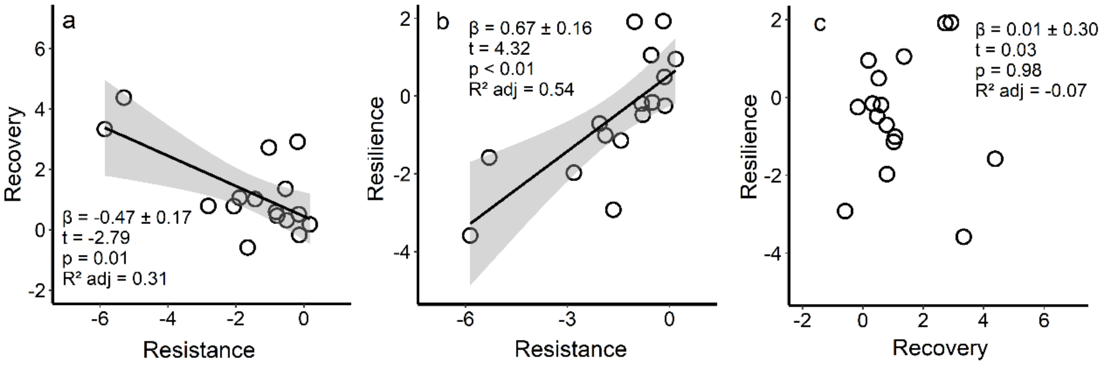
Figure 1 - Effects of experimental droughts on grasslands above-ground biomass.



Subtitle: Hedges'g effect sizes for resistance (**a**), recovery (**b**) and resilience (**c**) of grasslands above-ground biomass (N = 101) in response to experimental droughts. In studies reporting sequential drought events biomass data was averaged across all drought events. Negative/positive values indicate decreases/increases in biomass in treatment plots compared to control plots. Black dots/lines indicate mean effect sizes and its 95% confidence interval (CI). Q-statistics, degree of freedom (df); p-value and the proportion of the observed variance that reflects true differences among studies (I^2) testing for between-studies heterogeneity (compare to Fig. 3 in the main text where effect sizes were computed using biomass data only for the last experimental drought).

Source: The author, 2019.

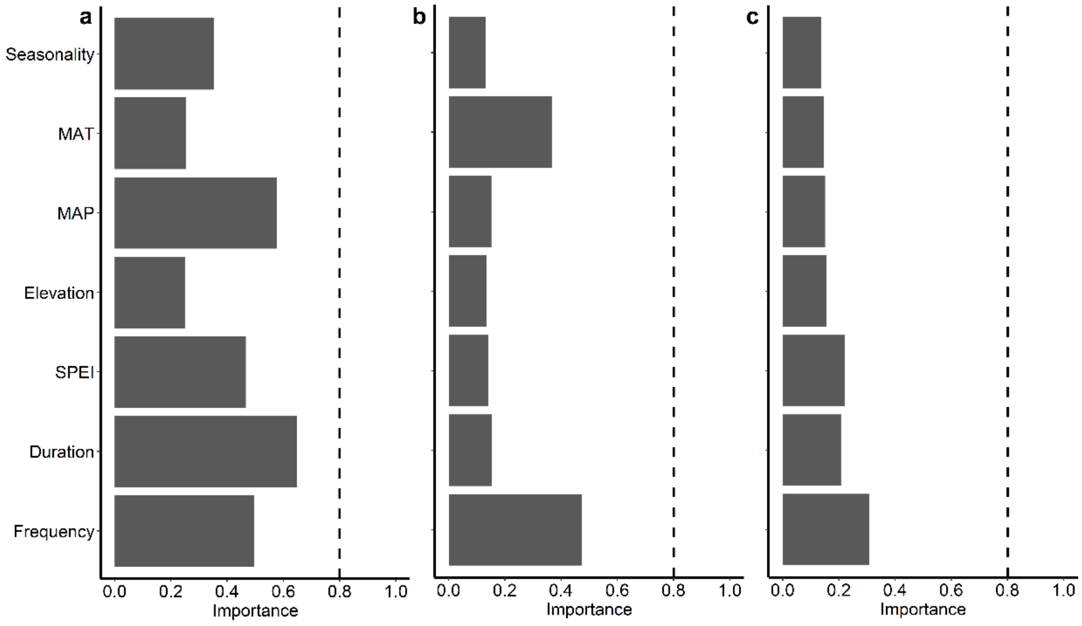
Figure 2 - Simple linear regressions testing for potential trade-offs among stability properties.



Subtitle: simple linear regressions testing for potential trade-offs among stability properties. Resistance, recovery and resilience were computed as Hedges'g effect sizes measuring the effects of experimental droughts on above-ground biomass of 106 grasslands. In studies reporting sequential drought events biomass data was averaged across all drought events (compare to Fig. 4 in the main text where effect sizes were computed using biomass data only for the last experimental drought).

Source: The author, 2019.

Figure 3 - Relative importance of seven moderators to explain variability in grasslands stability.



Subtitle: model-averaged importance of seven moderators explaining grasslands resistance (a), recovery (b) and resilience (c) in terms of above-ground biomass in response to experimental droughts. Moderators: rainfall seasonality (Seasonality, dimensionless); mean annual temperature (MAT, ºC); mean annual precipitation (MAP, mm); elevation (masl); standardized precipitation evapotranspiration index (SPEI) as a measure of drought intensity; drought duration (days); and drought frequency (number of sequential drought events). The vertical dashed line drawn at 0.80 can be used as a cut-off to identify important moderators. In studies reporting sequential drought events effect sizes were computed using biomass data only for the last experimental drought. In studies reporting sequential drought events biomass data was averaged across all drought events. Compare to Fig. 5 in the main text where effect sizes were computed using biomass data only for the last experimental drought.

Source: The author, 2019.

Table 3 - Checking for the effect of different approaches to compute effect sizes and to compute SPEI on the model-averaged importance of seven moderators explaining grasslandsstability in terms of above-ground biomass in response to experimental droughts.

Effectsize	**Moderator**	**Estimate ± 95% CI**						**Importance**	
		SPEI mean			**SPEI sum**			**SPEI mean**	**SPEI sum**
RT final	Seasonality	-0.69571	±	2.90612	-1.91865	±	5.41295	0.31	0.47
	MAT	0.01573	±	0.04810	0.01136	±	0.03972	0.43	0.37
	MAP	-0.00002	±	0.00024	-0.00002	±	0.00023	0.26	0.26
	Elevation	-0.00001	±	0.00011	-0.00001	±	0.00010	0.26	0.26
	SPEI	0.01125	±	0.13598	0.00026	±	0.01014	0.26	0.26
	Duration	0.00010	±	0.00044	0.00013	±	0.00055	0.30	0.31
	Frequency	-0.00849	±	0.06460	-0.00777	±	0.06565	0.27	0.26
RT averaged	Seasonality	-0.81938	±	2.98388	-3.06803	±	5.64318	0.35	0.68
	MAT	-0.00089	±	0.01376	-0.00316	±	0.01825	0.25	0.27
	MAP	-0.00034	±	0.00078	-0.00025	±	0.00063	0.58	0.51
	Elevation	-0.00001	±	0.00008	0.00000	±	0.00007	0.25	0.25
	SPEI	-0.13918	±	0.39843	-0.01650	±	0.03214	0.47	0.65
	Duration	0.00053	±	0.00104	0.00017	±	0.00072	0.65	0.38
	Frequency	0.05987	±	0.16227	0.03748	±	0.12923	0.50	0.39
RC final	Seasonality	-0.26356	±	4.30522	-0.12754	±	2.32767	0.16	0.13
	MAT	-0.01186	±	0.05013	-0.02222	±	0.07191	0.22	0.37
	MAP	0.00003	±	0.00047	-0.00008	±	0.00044	0.16	0.15
	Elevation	-0.00007	±	0.00031	-0.00001	±	0.00011	0.19	0.13
	SPEI	-0.14739	±	0.60441	-0.03220	±	0.22135	0.23	0.14
	Duration	0.00006	±	0.00082	-0.00010	±	0.00062	0.22	0.15
	Frequency	0.25028	±	0.37277	0.18861	±	0.50766	0.76	0.47
RC averaged	Seasonality	-0.20535	±	4.20767	-0.0869	±	2.20984	0.16	0.13
	MAT	-0.01254	±	0.05411	-0.0236	±	0.07671	0.22	0.36
	MAP	0.00008	±	0.00049	0.0000	±	0.00032	0.16	0.14
	Elevation	-0.00006	±	0.00030	0.0000	±	0.00010	0.19	0.13
	SPEI	0.00041	±	0.03214	0.0018	±	0.02235	0.22	0.17

	Duration	-0.00002	±	0.00061	-0.0001	±	0.00057	0.19	0.15
	Frequency	0.25854	±	0.40420	0.1974	±	0.52136	0.74	0.48
RS final	Seasonality	2.15811	±	7.84645	2.05869	±	7.60653	0.29	0.28
	MAT	0.02637	±	0.07299	0.02506	±	0.07155	0.46	0.44
	MAP	0.00008	±	0.00041	0.00007	±	0.00039	0.16	0.16
	Elevation	0.00001	±	0.00009	0.00001	±	0.00009	0.15	0.15
	SPEI	0.00804	±	0.14296	-0.00248	±	0.01688	0.14	0.17
	Duration	-0.00385	±	0.04421	-0.00231	±	0.00143	0.14	0.98
	Frequency	-0.00229	±	0.00147	0.00323	±	0.04230	0.97	0.14
RS averaged	Seasonality	-0.23979	±	3.76294	2.05869	±	7.60653	0.14	0.28
	MAT	0.00325	±	0.02831	0.02506	±	0.07155	0.15	0.44
	MAP	-0.00008	±	0.00059	0.00007	±	0.00039	0.15	0.16
	Elevation	0.00004	±	0.00023	0.00001	±	0.00009	0.16	0.15
	SPEI	-0.22845	±	0.95783	-0.00248	±	0.01688	0.22	0.17
	Duration	0.12020	±	0.42940	-0.00231	±	0.00143	0.31	0.98
	Frequency	0.00047	±	0.00203	0.00323	±	0.04230	0.21	0.14

Subtitle: resistance (RT), recovery (RC) and resilience (RS) in terms of above-ground biomass in response to experimental droughts. Effect sizes: final - computed using only the biomass data for the last drought event; or averaged - computed using biomass data averaged across all drought events; SPEI: averaged - SPEI values averaged for all the months within a drought event; or summed - SPEI summed for all the months within a drought event. Moderators: rainfall seasonality (Seasonality, dimensionless); mean annual temperature (MAT, ºC); mean annual precipitation (MAP, mm); elevation asl (m); standardized precipitation evapotranspiration index as a measure of drought intensity (SPEI); drought duration (days); and drought frequency (number of sequential drought events). 95 % CI: 95 % confidence interval for the estimates.

Source: The author, 2019.

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Supplementary Note C. Comparisons among stability indices used to assess grasslands above-ground biomass resistance, recovery and resilience in response to experimental droughts.

We classified stability indices in six groups (Table 1 in the main text), according to the type of stability property measured (resistance - RT; recovery - RC; resilience - RS; and relative resilience - RRS) and the calculation method used (group 1 - raw difference; group 2 - simple ratio; group 3 and 4 - compounded ratio; group 5 - natural logarithm ratio; group 6 - standardized ratio). Subsequently, we computed all the 19 indices using above-ground biomass data extracted from a subset of 101 grasslands (49 articles). In studies reporting sequential drought events, we calculated stability indices using only the biomass for the last drought event.

We found divergent conclusions about the differential stability across grasslands; that is, when grasslands were ranked according to their stability values, those rankings varied depending on the group of indices considered (Fig. 1). To better illustrate how and why results from different stability indices might not be comparable, we highlighted in the Fig.1 four study cases whose grasslands showed distinct stability responses: Carter and Blair 2012 (yellow); Yahdjian and Sala 2006 (green); Ingrisch et al. 2018 (red); and Shinoda et al. 2010 (blue). To facilitate understanding, we further referred to those studies by their corresponding colors in the Figure 1. Moreover, we restricted our following discussion only to resistance results, but we highlight that our further explanations would also be applicable for the other stability properties (recovery and resilience).

In group 1 indices, stability was merely obtained as raw differences in above-ground biomass between treatment and control plots. Consequently, results for those indices might be strongly influenced by the initial state of the system. That occurs because communities with higher initial biomass would always have more biomass to lose during drought and more biomass to recovery afterwards; thus, leading to lower resistance and potentially higher recovery and resilience for those communities in comparison to communities with lower initial biomass (Wang et al. 2007, Van Ruijven and Berendse 2010). Indices based on simple (group 2), compounded (groups 3 and 4) or natural logarithm ratios (group 5), could be used to avoid this problem, as they reported changes between treatment and control plots in proportional terms. Therefore, when comparing rankings of grasslands resistance among those groups of indices, similar results were found for proportional indices (groups 2, 3 and 5). All of them resulted in the following ranking: “yellow > red > green > blue”. However, a slightly different result was found for group 1 indices, as “red” and “green” studies switched positions: “yellow > green > red > blue”. That alteration occurred because grassland in the “red” study had a higher initial biomass than in the “green” study, thus leading to more biomass to be lost during drought and a lower resistance (RT1 more negative) in the former (RT1 red = -0.04) than in the latter grassland (RT1 green = -0.01). However, when the resistance was computed in proportional terms, for example using group 2 index, the proportion of biomass lost was actually higher and the resistance was lower (lower RT2) in the “green” (RT2 = 0.81) than in the “red” study (RT2 = 0.86).

In group 4 indices, stability was also calculated as a ratio, but their results were more complicated to interpret. For RT4 index, positive values indicate that biomass produced in drought plots was higher than in control plots (BD > BC, for example as in the “yellow” study); while negative values indicate that biomass was lost during drought. A value equal to -1 indicate that the system collapsed during drought (BD = 0). In scenarios of full resistance (BD = BC), however, those indices were undefined because they resulted in divisions by zero. Therefore, at a first moment, RT4 rankings seemed to largely differ from the other proportional indices (groups 2,3,5) but when correctly interpreted they actually shown the same result: “yellow > red > green > blue”.

Only group 6 indices expressed differences in above-ground biomass per unit change in precipitation. In the RT6 index, for instance, the magnitude of biomass changes between control and drought plots (BD/BC) was standardized by the magnitude of the drought treatment imposed (PPTD/PPTC). Thus, values equal to zero indicate that the system collapsed during drought (BD = 0), while progressively higher values indicate higher resistance. This standardization has been used to compare stability across studies that differed in the intensity of the precipitation treatment imposed, so that a conclusion about a lower stability for a certain system over other would not be merely because a greater proportional reduction in precipitation was imposed in the former (Shinoda et al. 2010). That is precisely what happened when comparing resistance between “red” and “green” studies. All other proportional indices (group 2-5) indicated that resistance was lower in “green” than in “red” study. However, when the resistance was standardized by the drought intensity, as the drought was more intense in the “green” than in the “red” study, we actually found a larger resistance in the former study (“green” >> “red”). Therefore, the apparent lower resistance of the "green" study over the "red" might be merely related to an experimental drought of higher intensity imposed in the former study. However, it has been showed that the percentage of rainfall intercepted is not a reliable index of experimental drought intensity, since it could be highly influenced by interannual precipitation variability an would be not comparable across sites with distinct precipitation regimes (Hoover et al. 2018, and see also Fig. 1 in the main text).

Regarding the resilience indices, studies have measured this property using two distinct approaches: resilience per se (RS1 to RS5) and relative resilience (RRS1, RRS2). Resilience per se indices quantified the ability of grasslands to reach non-drought biomass levels after drought alleviation; thus, a grassland would be considered resilient whenever non-significant differences were detected between control and drought plots during the post-drought period (BCpd = BDpd). Alternatively, relative resilience indices quantified whether, during the post-drought period, grasslands would be able to recover all the biomass previously lost during the drought. Thus, in relative resilience indices the resilience is weighted by the degree of damage incurred during the drought (i.e. RS is weighted by RT; Ingrisch et al. 2018b). For example, in the RRS1 index the higher the amount of biomass lost during drought, that is, the lower the resistance (lower values for the term BD/BC), the higher the relative resilience.

Surprisingly, any of the selected articles have assessed resilience as the recovery time, that is, as the amount of time needed for the above-ground biomass in the drought plots to achieve values similar to the control plots (engineering resilience; Gunderson 2000). Finally, we highlight that group 6 indices were not calculated for resilience because during the post-drought period the precipitation inputs were equal for drought and control plots. Consequently, the term PPT treatment/ PPT control would always be equal to zero and hence RS6 would always result in an undefined division by zero.

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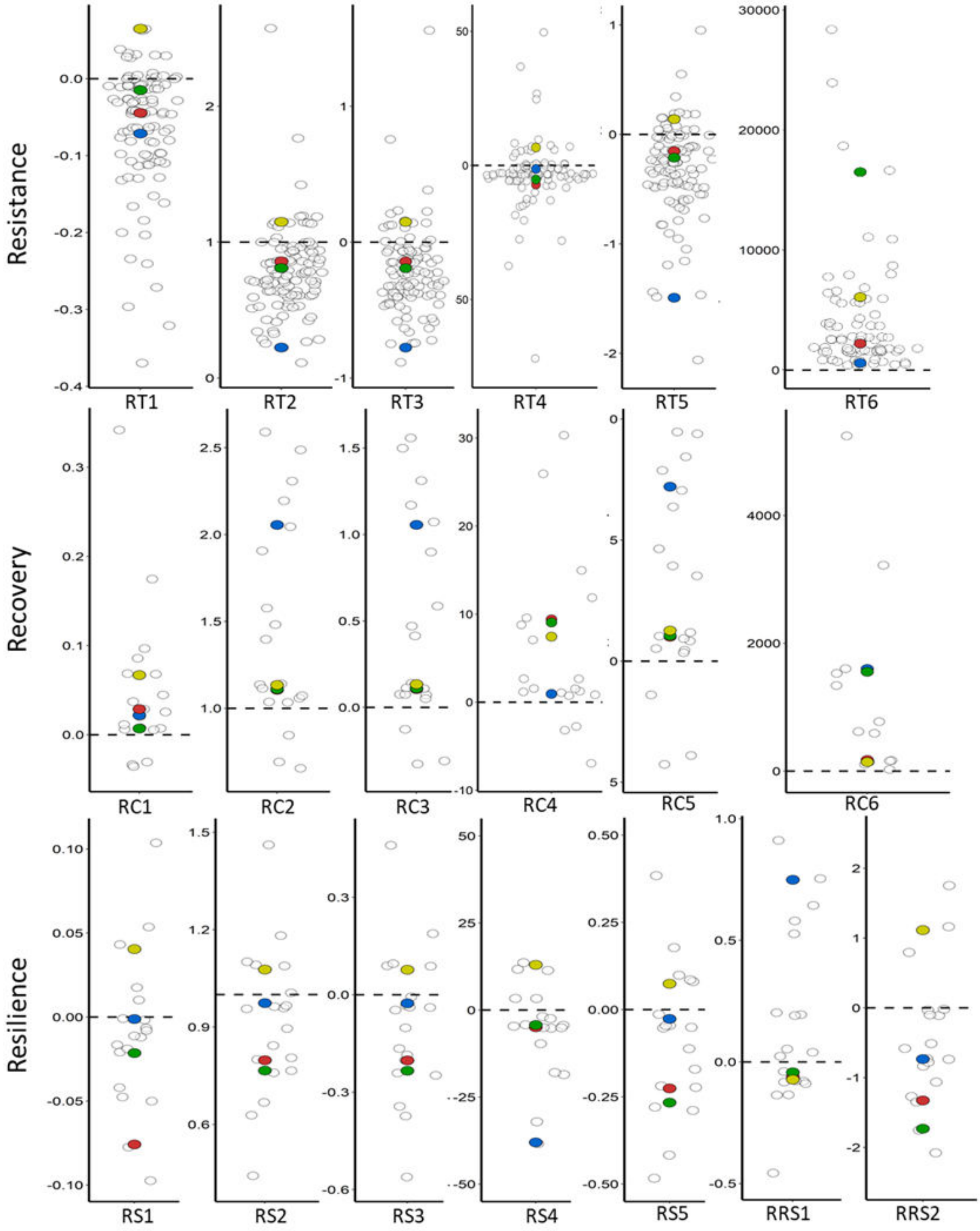
Figure 1 - Comparisons acrossstability indices used to assess grasslands stability.



Subtitle: stability indices used to assess resistance (RT1 - RT6, n = 101), recovery (RC1 - RC6, n = 19) and resilience (RS1 – RRS2, n = 19) of grasslands above-ground biomass in response to experimental droughts. In studies conducting sequential drought events indices were computed using only the biomass data for the last drought event. Four study cases were highlighted (yellow: Carter and Blair 2012; green: Yahdjian and Sala 2006; red: Ingrisch et al. 2018; and blue: Shinoda et al. 2010) to better illustrate the inconsistences among different stability indices. Dashed black lines indicate values for full resistance; no recovery and full resilience (excepted for class 5 indices which values are undefined for those situations). Points were jittered to reduce overlapping.

Source: The author, 2019.

Table S1 - Results of simple meta-regressions testing the effects of moderators related to experimental characteristics (vegetation type; shelter area; shelter type; and control plot type) on the Hedges' g effect sizes for grasslands resistance (RT), recovery (RC) and resilience (RS) in response to experimental droughts.

Moderator	**Effect size**	**AICc**	**T²**	**I²**	**R²**	**F or Q**	**df**	**p-value**	**Estimate [95% CI]**
Vegetation type	RT final	323.05	1.0499	71.6900	0.0000	1.4011	2	0.4963	Manipulated -1.2105 [-1.7856; -0.6355] a Natural -1.3623 [-2.6723; -0.0523] a Seminatural -0.3136 [-2.272; 0.2614] a
	RT averaged	318.40	0.7489	65.2300	0.0000	1.0034	2	0.6055	Manipulated -1.1573 [-1.6626; -0.6520] a Natural -0.9461 [-2.0719; 0.1796] a Seminatural -0.8429 [-1.9633; 0.2775] a
	RC final	78.09	1.9441	80.4000	0.0000	2.1089	2	0.3484	Manipulated 1.9005 [0.0154; 3.7857] a Natural 1.3972 [-2.6375; 5.432] a Seminatural 0.4156 [-3.7437; 4.575] a
	RC averaged	54.41	0.7490	57.7300	0.0000	2.2736	2	0.3208	Manipulated 1.7738 [0.4568; 3.0909] a Natural 0.8884 [-1.9054; 3.6823] a Seminatural 0.5372 [-2.3920; 3.4665] a
	RS final	49.21	0.0000	0.0000	100.0000	10.5828	2	0.0050	Manipulated 0.5359 [-0.2220; 1.2938] a Natural -0.7199 [-2.3243; 0.8845] b Seminatural 0.0126 [-1.6845; 1.7096] a
	RS averaged	60.38	1.4500	78.1000	0.0000	1.6574	2	0.4366	Manipulated 0.4391 [-1.1741; 2.0523] a Natural -0.7822 [-4.2671; 2.7027] a Seminatural -0.3545 [-4.0200; 3.3110] a
Shelter area (m²)	RT final	367.17	1.1810	74.5600	4.1000	4.1657	97	0.0440	-0.0041 [-0.0081; -0.0001]
	RT averaged	356.60	0.7799	66.5900	11.0500	8.9419	102	0.0035	-0.0063 [-0.0104; -0.0021]
	RC final	69.31	1.1976	74.4000	36.8300	2.4358	15	0.1394	0.0034 [-0.0013; 0.0081]
	RC averaged	42.52	0.1213	25.6500	66.2100	3.4446	12	0.0882	0.0030 [-0.0005; 0.0065]
	RS final	51.61	0.1957	33.5100	0.0000	0.0602	15	0.8096	0.0003 [-0.0021; 0.0027]
	RS averaged	47.74	0.8708	70.9500	29.4000	4.1338	12	0.0648	-0.0036 [-0.0075; 0.0003]
Shelter type	RT final	376.40	1.1701	74.1500	2.2600	2.3717	1	0.1235	Automatic -2.0491 [-3.2565; -0.8417] a Permanent -1.0775 [-3.5214; 1.3665] a
	RT averaged	374.28	0.8727	68.7000	0.0000	0.0119	1	0.9132	Automatic -0.9754 [-1.8775; -0.0733] a Permanent -0.9235 [-2.7579; 0.9109] a
	RC final	74.69	1.3775	75.8100	21.3200	4.1361	1	0.0420	Automatic 4.1567 [1.1048; 7.2086] a Permanent 0.9159 [-5.2593; 7.091] b
	RC averaged	NA	NA	NA	NA	NA	NA	NA	only permanent shelters
	RS final	44.40	0.1136	22.2500	17.5800	9.6120	1	0.0019	Automatic -4.4387 [-7.0614; -1.8159] a Permanent -0.2561 [-5.5229; 5.0209] b
	RS averaged	NA	NA	NA	NA	NA	NA	NA	only permanent shelters
Control plot type	RT final	369.26	1.0254	71.3800	14.3400	10.1393	1	0.0015	Ambient -0.9188 [-1.1939; -0.6437] a Historic -1.9767 [-2.903; -1.0505] b
	RT averaged	366.42	0.8529	64.5800	14.7500	8.3291	1	0.0039	Ambient -0.7642 [-1.0007; -0.5278] a Historic -1.5986 [-2.4017; -0.7955] b
	RC final	78.41	1.8359	79.8000	0.0000	0.7964	1	0.3722	Ambient 0.9432 [0.1123; 1.7740] a Historic -1.7072 [-0.8017; 4.2160] a
	RC averaged	54.11	0.5355	56.7200	0.0000	0.0026	1	0.9590	Ambient 0.9013 [0.3170; 1.4857] a Historic 0.9301 [-0.7530; 2.6133] a
	RS final	55.14	0.3719	24.8000	0.0000	0.5270	1	0.4679	Ambient -0.3937 [-0.7865; -0.0009] a Historic -0.0979 [-1.2893; 1.0936] a
	RS averaged	59.41	1.4828	78.2900	0.0000	0.5644	1	0.4525	Ambient -0.6089 [-1.4389; 0.2180] a Historic -0.0306 [-2.3663; 2.3049] a

Subtitle: in studies reporting sequential drought events effect sizes were computed either using biomass data only for the last experimental drought (final; 49 articles and 101 study cases) or using biomass averaged across sequential drought events (averaged; 54 articles and 106 study cases). AICc: second-order Akaike information criterion (AICc); T²: between studies variance; I²: percentage of the observed variance that reflects true differences among studies; R²: percentage of the true variance explained by the moderator; F or Q statistics and p-value for quantitative and qualitative moderators, respectively; df: degree of freedom; Estimate parameter [95 % confidence interval].

Source: The author, 2019.

2 O EFEITO DA DIVERSIDADE FUNCIONAL

> Strength lies in differences, not in similarities.
>
> *Stephen R. Covey*

2.1 Integrating eco-physiological strategies and functional originality indices to predict plant community stability in response to droughts

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2.1.1 Abstract

A future climate with more extreme droughts might exacerbate the global biodiversity crisis by increasing local species extinctions. Identifying which species would be more prone to extinction, and which properties could regulate their differential stability is, therefore, essential to predict the effects of dryer conditions over plant communities. Broad-scale ecological approaches, such as Grime's CSR scheme (C: competitor/ S: stress-tolerant/ R: ruderal) employs economic and regenerative traits to predict species responses to both disturbances and stresses; whereas physiological approaches, such as Levitt's scheme (avoidance/tolerance/escape) uses regenerative and hydraulic traits in order to provide a more mechanistic explanation of how plants respond to resource shortages. Here we proposed a unified framework to identify plant strategies in response to drought, and used functional originality indices (which describes how co-existing species are distributed within and across strategies) to assess the consequences of species loss on the community vulnerability to functional homogenization (loss of functional originality). We measured economic, hydraulic and regenerative traits in 51 plant species (herbs and shrubs) from a mountain tropical grassland and computed their functional originality, in order to: evaluated the existence of trade-offs among those traits; identify eco-physiological strategies of response to drought; and assess the community vulnerability under distinct scenarios of species loss. We demonstrated that traits co-vary defining two main trade-offs (resistance vs. recovery and water-storage vs. water-absorption), and three eco-physiological strategies: S-tolerator; CR-escapers/avoiders; and CS-escapers/avoiders. Functional originality was unevenly distributed across species and strategies. Consequently, community vulnerability differed depending on the scenario of species loss. The extinction of S-tolerators and CR-escapers/avoiders species resulted in greater impacts on the community than the loss of CS species.

Synthesis: The integration of eco-physiological strategies and functional originality indices in a single approach, as proposed here, is a promising tool to anticipate the effects of droughts on plant communities, and so to assign conservation priorities.

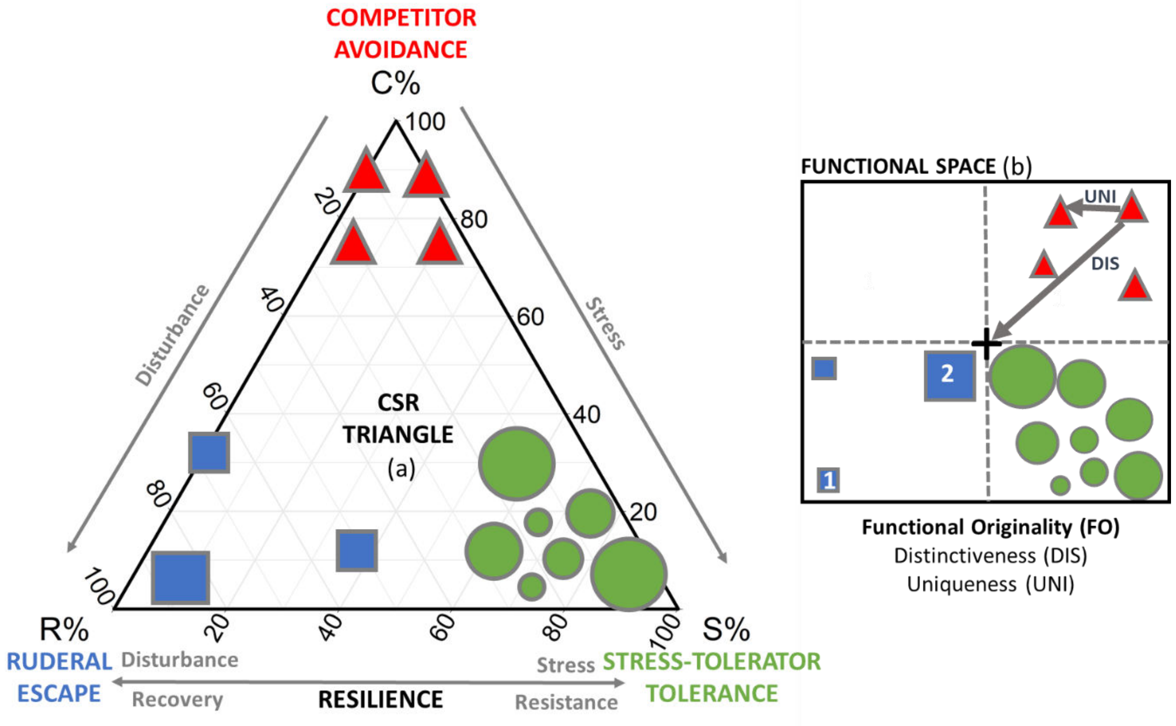
Keywords: CSR theory, dehydration avoidance, dehydration escape, dehydration tolerance, functional redundancy, recovery, resistance, resilience.

2.1.2 Introduction

Extreme droughts are predicted to increase in many regions due to both decreases in rainfall amounts and altered rainfall seasonallity (Huang et al. 2006). Identifying plants traits that determine their ability to withstand drought without loss of function (resistance) or to recover function when water deficits are relieved (recovery) is, therefore, increasingly important to predict and model community stability under future drier conditions (Griffin-Nolan et al. 2018). Although certain traits, such as stem and leaf vulnerability to cavitation (Maherali et al. 2004, Blackman et al. 2012) and leaf water potential at the turgor loss point (Ψ_{tlp}; Bartlett et al. 2014), have been pointed out as good proxies; plants response to drought is a complex phenomenon, and might be better described by a combination of multiple traits (Pivovaroff et al. 2016), rather than by one single trait. Co-existing species may exhibt distinct strategies (i.e. grouping of traits and responses among species which cause them to exhibit ecological similarities, Grime 2001) to cope with droughts. Classically, two distinct approaches, ecological and physiological, have been applied to determine plant strategies in response to resource shortages, including droughts (Fig. 1).

The CSR theory, proposed by Grime (1977) is one of the most widely adopted ecological approaches (Pierce et al. 2017) and has a strong parallel with the ‘fast-slow’ plant economics spectrum (Wright et al.2004, Reich 2014). According to this theory, species can be positioned in a CSR triangle (Fig. 1a), based on their proportions of each of the three primary ecological strategies: competitor (C%), stress-tolerator (S%) and ruderal (R%). Competitor species are tall, long-living organisms that exhibit an acquisitive strategy, and an intermediate position along the 'fast-slow' economic spectrum. Their economic traits (large leaf area -LA andspecific leaf area -SLA, but low leaf dry matter content -LDMC) allow them to maximise the capture of resources, the vegetative growth, and the competitive ability, in productive and undisturbed conditions. Contrarily, stress-tolerator species are short, slow-growing, long-living organisms that show a conservative resource-use strategy ('slow' economic traits: small LA and SLA, but high LDMC) to enable the preservation of metabolic processes and survival, at the expense of both vegetative and reproductive growth, under stressful conditions. Finally, ruderal species are short (small LA), fast-growing, short-living organisms ('fast' economic traits: large SLA and low LDMC) that invest mainly in reproductive growth (seed production) to ensure a fast recovery after disturbances (Grime 1977, 2001, Pierce et al. 2013, 2017).

Figure 1 - Framework integrating eco-physiological strategies and functional originality indices to predict community vulnerability to functional homogenization.



Subtitle: (a) -eco-physiological strategies in response to drought defined by the integration of CSR ecological strategies (competitor - C; stress-tolerator - S; ruderal - R) and physiological strategies (avoidance; tolerance; escape); (b) -functional originality indices (FO) defined by species position in the functional space, distinctiveness (DIS) is the distance of a target species from the center of the functional space and uniqueness (UNI) is the distance from the nearest neighbour. Number 1 indicates a distinct and unique species, while 2 indicates an indistinct and redundant species. In (a) and (b) each point represents a species, shape and colors indicate different eco-physiological strategies and size indicates species frequency in the community.
Source: The author, 2019.

Although the CSR scheme is useful to predict whether plants would be able to cope with water shortages or not, it lacks a more detailed explanation of why and how species in different strategies respond to drought as they do (Volaire et al. 2018). For instance, one of the criticisms about this theory is that despite succulent and sclerophyll species dealing with low water availability through very different ways, they represent converging strategies in terms of resource-use (both are conservative with a preferential allocation to storage rather than to growth) and hence both would be classified as stress-tolerators (Wilson and Lee 2000, Pierce et al. 2013).

Physiological approaches, in turn, describe plantsresponse to drought in a more mechanistic way by including hydraulic traits (Brodribb 2017, Griffin-Nolan et al. 2018). Those traits reflect physiological functions directly related to water-availability, such as plants ability to control gas exchange and to ensure the integrity of their hydraulic system under water deficit (e.g. Sack and Holbrook 2006, Choat et al. 2012, Klein et al. 2014). The scheme proposed by Levitt (1972) is one of the most used physiological approaches. According to this scheme, dehydration tolerator plants possess a set of hydraulic traits (e.g. anisohydric behavior, more negative Ψ_{tlp} and low xylem vulnerability to cavitation) that allow continued water transport and gas exchange under progressively lower water potentials in the plant tissues (Engelbrecht and Kursar 2003, Brodribb et al. 2014; Pausas et al. 2015). Contrarily, dehydration avoiders are able to maintain tissue water potentials as high as possible during drought, what can be achieved either by minimizing water loss (e.g. isohydric behaviour), by maximizing water uptake (e.g. deep rooting), by storing water in modified tissues (e.g. succulence) or by exhibiting a more efficient water transport (Chaves et al. 2003). Finally, dehydration escape is mainly defined by phenological (e.g flowering onset) and regenerative traits (e.g. seed size) that enable a plant to ‘escape’ dehydration in time by completing its life cycle before the onset of severe water deficit and hence by surviving the dry period as dormant seeds (Farooq et al. 2009), oralternatively, as dormant meristematic tissues, whose stored resources are further used for resprouting after drought (Pausas et al. 2015).

Relationships among economic and hydraulic traits are still controversial. Some studies have suggested that hydraulic traits are decoupled from the economic spectrum and might constitute independent axes of variation (e.g. Sack et al. 2013; Li et al. 2015), while others support a close relationship among them, at both leaf (e.g. Villagra et al. 2013) and stem levels (e.g. Santiago et al. 2018). If plant economic, hydraulic and regenerative traits were indeed correlated across leaf, stem and root systems, then it would be possible to integrate the above ecological and physiological approaches in a unified framework of plant functional response to drought (Volaire et al. 2018). According to this framework, the ‘slow’ economic traits of the stress-tolerator species would enable them to move and use less water and to have dense tissues, characteristics that would also promote a high dehydration tolerance (S-tolerator); while the ‘fast’ economic traits of both competitors and ruderal species would maximize water acquisition, leading to a dehydration avoidance strategy in the former species (C-avoider); and a higher investment in seed production to facilitate dehydration escape in the latter species (R-escaper) (Fig. 1a; Reich 2014, Berger et al. 2016, Volaire et al. 2018).

In the context of this framework, a drought event could be considered either a stress (if the drought restricts plants growth) or a disturbance (if the drought causes partial or total destruction of plant biomass) depending on its intensity, duration and frequency, as well as, on its primarily effects on plant function (Grime 2001, Berger et al. 2016). Species would respond to drought in terms of resistance (defined here as the ability to maintain biomass production during the drought; Mariotte et al. 2013), or recovery (defined as the ability to produce new biomass after the drought alleviation to compensate for the biomass lost during the drought; Mariotte et al. 2013). Resistance and recovery might constitute two alternative ways for plants to achieve resilience, i.e. to return to their original biomass state when water deficits are relieved (Mariotte et al. 2013); and a trade-off would be expected between those two properties at least at the individual level (Grime 2001).

Once the eco-physiological strategies of co-existing species were properly identified it would be possible to determine the functional originality of the community, as it depends on how many strategies co-exist, and on how the species are distributed within and across thosestrategies (Fig. 1b; Rosenfeld 2002). Functional originality might be assessed based on species position in the functional trait space (Fig. 1b), through two main indices:

distinctiveness (DIS) and uniqueness (UNI). DIS corresponds to the distance of a target species to the center of the functional space, and thus reflects how different the trait-combination possessed by that species is, compared to the average traits in the community; while UNI is the distance of a species to the nearest neighbour in the functional space, and thus indicates if the trait-combination possessed by that species is exclusive or shared with other co-existing species (Buisson et al. 2013, Mouillot et al. 2013).

The extinction of a distinct and unique species (Fig. 1b, n°1) would necessarily lead to a reduction in community originality (Clavel et al. 2011), while the loss of an indistinct and redundant species (Fig. 1b, n°2) would have less impact on the community, since there would be other redundant species that could compensate for its loss. Simulations of different scenarios of species extinctions could then be used to estimate the effects of drought on the community vulnerability to functional homogenization (i.e. vulnerability to the loss of functional originality, Clavel et al. 2011). If the most original species are more prone to extinction (i.e. more sensitive to drought), then droughts events could lead to an initial faster decline in functional originality, because the extinction of only a few species would result in the loss of irreplaceable traits. Alternatively, if less original species are more sensitive, then the initial drought impact would be limited, due to the presence of redundant species (species that exhibit similar combination of traits).

Although eco-physiological strategies and functional originality indices are compelling approaches for predicting plantsresponse to drought, few attempts have been made to apply them conjunctly to entire communities, possible because of the labour-intensive methodologies required to measure hydraulic and regenerative traits for a large number of co-existing species (Brodribb 2017, Griffin-Nolan et al. 2018). In this study we aimed at identifying the eco-physiological strategies in response to drought of a tropical mountain grassland community. We measured economic, hydraulic and regenerative traits (Table 1) of 51 plant species (herbs and shrubs) in order to assess the possible trade-offs among those traits (i.e resistance vs. recovery strategies). We also evaluated how the functional originality was distributed among species and across strategies, and the implications of those distributions on the community vulnerability to functional homogenization under distinct scenarios of species loss. The remarkable spatial heterogeneity of this mountain landscape, may enable the co-occurrence of plants with distinct abilities to cope with drought (Porembski 2007). Therefore, we might expect to identify the co-existence of distinct eco-physiological strategies and also to support a trade-off between resistance and recovery strategies. We predict that originality would vary independently of species sensitivity to drought, and thus losing species in different strategies would result in similar effects on community vulnerability to functional homogenization.

Table 1 - Functional meaning of economic, hydraulic and regenerative traits.

Trait	Abbr.	Unit	Functional meaning
Economic			
Leaf area	LA	mm^2	One-sided area of an individual leaf; Smaller LA decreases the transpiring leaf surface and thereby the rate of water loss during drought (Markesteijn and Poorter 2009).
Leaf dry matter content	LDMC	%	Leaf dry mass divided by its water-saturated fresh mass; Higher LDMC is linked to slower relative growth rate, longer leaf lifespan, a conservative resource-use strategy, and to the presence of thicker and more rigid cell walls, enabling the maintenance of turgor and minimizing cell damage during drought (Engelbrecht and Kursar 2003).
Leaf succulence	SUC	$g\ H_2O\ dm^{-2}$	The capacity for leaf water storage, measured as (saturated leaf mass - leaf dry mass)/leaf area; Higher SUC enables a plant to maintain relatively higher water potentials and avoid dehydration as the soil dries out (Kluge and Ting 1978, Vendramini et al. 2002).
Specific leaf area	SLA	$mm^2\ mg^{-1}$	One-sided leaf area divided by its dry mass; SLA represents the construction cost of a unit leaf area. Lower SLA under drier conditions could be linked to drought-resistance through a conservative resource-use strategy, or to drought-avoidance through water storage (succulence) (Vendramini et al. 2002, Wright et al. 2004).
Stem specific density	SSD	$mg\ mm^{-3}$	Stem dry mass divided by its fresh volume; It describes the carbon investment per unit volume of stem; Higher SSD is linked to an increased cavitation resistance, but a reduced hydraulic conductivity, stem water storage capacity, and cavitation recovery in response to drought (Pockman et al. 2001, Santiago et al. 2018).
Hydraulic			
Foliar water uptake	FWU	%	The movement of water coalesced on the leaf surface into the leaf; Higher FWU may enable the maintenance of leaf hydration and gas exchange when leaf-wetting events occur simutaneouly to dry soil conditions (Limm et al.2009).
Stomatal density	SD	$n° mm^{-2}$	Number of stomata per unit of leaf area; Lower SD under severe drought may occur due to the inhibition of guard cell differentiation, and may result in lower stomatal conductance, thereby reducing water loss; on the other hand, higher SD under moderate drought may reduce transpiration by a quicker onset of stomatal regulation (Xu and Zhou 2008).
Venation density	VD	$mm\ mm^{-2}$	Length of minor veins per unit of leaf area; Higher VD can enable higher leaf hydraulic conductance, higher rates of gas exchange per unit leaf area, and greater tolerance of vein blockage during drought (Sack and Scoffoni 2013).

Average fraction of the leaf surface allocated to stomatal pores	Fsp	%	The stomatal density multiplied by the average anatomical maximum stomatal pore area. A higher Fsp could potentially lead to a higher water loss when all stomata are completely open.
Maximum midday stomatal conductance	$g_{s\ md}$	mmol m^{-2} s^{-1}	A measure of the water loss from plant leaves controlled by stomatal aperture; Lower g_s in plants subjected to drier conditions minimizes the water loss and avoids extremely negative water potentials, which could result in desiccation damage and high level of xylem embolism, but also reduces the carbon absorption and photosynthetic capacity (Franks et al. 2007).
Iso-/anisohydric behaviour	Δslope	-	The slope of a linear regression fitted to a plot of log (pre-dawn leaf water potential Ψ_{pd}- midday leaf water potential Ψ_{md}) vs. Ψ_{pd}, with anisohydric species showing lower slopes; Isohydric species are those that maintain a roughly constant Ψ_{md} regardless of Ψ_{md}, possibly because of their stricter stomatal control, thereby maintaining a high water potential, but at the risk of death due to carbon starvation; whereas anisohydric species exhibit progressively lower Ψ_{md} as a function of lower Ψ_{pd} , possibly because they keep their stomata open at low water potentials, thus maintaining carbon assimilation, but at the risk of failure in the water transport due to xylem cavitation (Franks et al. 2017).
Leaf water potential at the turgor loss point	Ψ_{tlp}	MPa	The negative water potential at which leaf cells lose turgor; More negative Ψ_{tlp} is linked to drought-resistance and the leaf capacity to maintain its stomatal conductance and photosynthetic gas exchange under drier conditions; Less negative Ψ_{tlp} may be related to drought-avoidance and the leaf capacity to maintain a high relative water content at the turgor loss point (Hochberg et al. 2018, Bartlett et al. 2012, Meinzer et al. 2016).
Regenerative			
Seed size	SS	cm	The longest dimension of the seed; Larger SS promotes larger initial seedling size and thus a higher probability of seedling establishment. Conversely, smaller seeds can result in a longer persistence in the seed bank and in longer dispersal capacity (Leishman and Westoby 1994, Khurana et al. 2006).
Resprout ability	RA	%	The relative ability of a plant species to form new biomass after the destruction of most of its above-ground biomass by using reserves from basal or below-ground plant parts; Species that grow in drier environments are expected to resprout more vigorously than in moister areas, especially because opportunities for seedling establishment are limited under dryer conditions (Pausas et al. 2015).

Source: The author, 2019.

2.1.3 Material and Methods

2.1.3.1 Study area and species

This study was carried at a mountain tropical grassland (*Campos de Altitude*) located in the Itatiaia National Park (INP) (22º22'37" S, 44º42'28" W, above 2, 400 m asl), between the Rio de Janeiro and Minas Gerais states, Brazil. The climate is tropical of altitude (Cwb - Köppen), with mean annual temperature of 14.4 °C and mean annual precipitation about 2, 200 mm (Segadas-Vianna and Dau 1965). Rainfall is markedly seasonal, with a rainy summer (Dec to Mar) and a dry winter (Jun to Aug). Summer dry spells can also occur, especially in El Niño years (Safford 1999) and are often associated with the occurrence of fires (Aximoff and Rodrigues 2011). Besides drought, plants are subjected to harsh winds, low temperatures, frost and high solar radiation, and they grow on shallow, unfertile and rocky soils (Safford 1999).

The vegetation is composed of shrubs sparsely distributed in an herbaceous matrix co-dominated by the bunchgrass *Cortaderia modesta* (Döll) Hack. ex Dusénand the Cyperaceae *Machaerina ensifolia* (Boeckeler) T. Koyama (Camerik and Werger, 1981). A frequency survey using the quadrat method (Coulloudon et al. 1996) was conducted during the summer to support the choice of species to be sampled for the trait measurements. To best represent the diversity of plant strategies to cope with drought we selected 51 species (Table S1), including diferent life-forms (grasses, forbs and shrubs) and dominances (rare and dominant).

2.1.3.2 Trait measurements

Economic traits: branchlets (whole individual for herbs) from 10 individuals per species were collected and rehydrated for 2 h. Five mature leaves (excluding the petiole) were sampled per individual to determine the water saturated fresh mass (0.01 g), then leaves were scanned (300 dpi resolution) to obtain the leaf area (LA), using the software Image J version 1.48, and oven-dried at 50 °C for 72 h to determine the dry mass. LA, fresh and dry mass were then used to obtain specific leaf area (SLA), leaf dry matter content (LDMC), and leaf succulence (SUC) (see Table 1). To determine the stem specific density (SSD), a 5 cm stem section was cut, had its bark removed, and was submersed in water for 30 min. Next, the fresh volume was obtained, following the Archimedes principle of water displacement, and the stem was oven-dried for five days at 60 °C (Rosado and de Mattos 2010).

CSR strategies: CSR percentages for each species were computed using the 'globally-calibrated CSR strategy calculator tool StrateFy' (Pierce et al. 2017). In the StrateFy the

LDMC, SLA, and LA of each species were compared against the axes of a multivariate space occupied by 3, 068 tracheophytes, thus returning the relative percentage of competitiveness (C %), stress-tolerance (S %) and ruderalism (R %) for each species (Pierce et al. 2017). We further used those results to select a subset of 12 species for the measurement of hydraulic and regenerative traits (*Achyrocline satureioides* (Lam.) DC.; *Baccharis uncinella* DC.; *Chionolaena capitate* (Baker) Freire; *Chusquea pinifolia* (Nees) Nees; *C. modesta*; *Eryngium glaziovianum* Urb.; *Gamochaeta purpurea* (L.) Cabrera; *Hypochaeris lutea* (Vell.) Britton; *Leptostelma maximun* D. Don; *M. ensifolia*; *Mikania glaziovii* Baker; and *Pleroma hospital* (Schrank et Mart. ex DC.) Triana). Those species were selected in order to represent the range of variation of CSR % in the evaluated community.

*Hydraulic traits:*foliar water uptake (FWU), was measured on five individuals per species following methods from Limm et al. (2009). Samples (branches or whole individual) were collected and rehydrated at 5 °C in darkness for 72 h. Next, one mature healthy leaf per branch was excised and dried on a bench for 3 h at 20 °C. The leaf was weighed (m_1) and then the petiole was sealed with vaseline to prevent water entry. The whole leaf lamina was submersed in distilled water in darkness. After 3 h, the leaf was dried with paper towels and reweighed (m_2). To account for any potential error associated with residual water on the leaf surface, the leaf was allowed to dry on a bench for 5 min and then weighed (m_3). The same leaf was re-submersed in water for 1 s, dried with paper towels and immediately reweighed (m_4). This brief re-wetting did not allow sufficient time for water absorption, so any increase in mass associated with this second submersion represented the residual water on the leaf surface. All leaves were oven-dried for 72 h for determination of the dry mass (m_{dry}). The FWU was calculated as follow: $FWU = [(m_2-(m_4-m_3)-m_{dry})/(m_1-m_{dry})] * 100\ \%$, where the ($m_4$-$m_3$) term was used as a correction for residual water on the leaf surface.

To obtain stomatal and venation traits, one leaf of five individuals per species was sampled, subjected to the diaphanisation technique (Strittmater 1973) and mounted on glass slides. Digital photographs of both abaxial and adaxial leaf surfaces were taken up to a total of 1 mm^2 of area sampled per leaf surface, using a digital camera coupled in a light Microscope (Olympus Cx40, Spectra Services, Ontario, USA). The digital images were then analysed using the software Image Pro Plus version 4.5, to obtain: stomatal density (SD), venation density (VD), and the average fraction of the leaf surface allocated to stomatal pores (Fsp).

Leaf water potential at predawn (Ψ_{pd}) and midday (Ψ_{md}) and midday stomatal conductance were monthly measured (from June 2016 to June 2017), on two individuals per species using a leaf porometer (model SC1, Decagon Devices, Pullman, WA, USA) and a Scholander chamber (model 1505D-EXP, PMS, Albany, OR, USA), respectively. From those data, we computed the maximum midday stomatal conductance ($g_{s\ md}$) and the iso-/anisohydric behaviour (Δslope; Meinzer et al. 2016). Besides, the leaf water potential at the turgor loss point (Ψ_{tlp}) was obtained from pressure–volume curves generated for five individuals per species during the dry season (Jun-Aug 2017), by using the bench drying technique (Turner, 1988) and a fitting routine based on Sack and Pasquet-Kok (2011).

Regenerative traits: seeds were monthly collected (2016 to 2017) from five individuals per species and then five seeds per individual were observed at a stereomicroscope to obtain the seed size (SS). Resprout ability (RA) was experimentally obtained in the mid-May 2017 (period before the dry season) for five individuals per species by clipping and oven-drying the aboveground biomass (at 50 °C for eight days) to obtain the initial dry aboveground biomass (Bi). One year later, individuals were resampled to obtain the resprouted dry aboveground biomass (Br). The resprout ability was computed as RA = Br*100/Bi (Moreira et al. 2012).

2.1.3.3 Identifying the eco-physiological strategies

Because not all traits were measured for all species we conducted a Bayesian hierarchical probabilistic matrix factorization (BHPMF; Schrodt et al. 2015), which imputed missing values based on both the taxonomic hierarchy and the correlation structure within the matrix of species versus $\log_{10}$-transformed trait values. The imputed values were then used in a principal component analysis (PCA) to assess the trade-offs among traits, and in a hierarchical agglomerative cluster analysis, based on Euclidean distances and the Ward's linkage, to identify the eco-physiological strategies.

2.1.3.4 Evaluating the impacts of species loss scenarios

Functional originality (FO) indiceswere computed for the 51 plant species, as follow: uniqueness (UNI), was obtained as the Euclidian distance of a target species to the nearest neighbour in the PCA; and distinctiveness (DIS), as the Euclidean distance of a target species to the PCA center. FO indices were standardized dividing them by the respective maximum value. Thereby, all three FO indices ranged from 0 (lowest originality) to 1 (highest originality) (Mouillot et al. 2008, 2013, Buisson et al. 2013, Violle et al. 2017).

We evaluated the effects of losing all the species within each eco-physiological strategy on the community vulnerability to functional homogenization. Thus, for each strategy we computed the community UNI and DIS after excluding all species within that strategy, and then simulated (1, 000 times) random scenarios where the same number of species were lost. Finally, we computed standardized effect sizes [SES = (mean FO random – mean FO non-random)/ standard deviation FO random] to assess whether the scenarios of losing strategies differed from a random species loss.

2.1.3.5 Statistical analysis

Kruskall-Wallis rank sum test and median tests were used to evaluate whether CSR % and FO indices differed among theeco-physiological strategies. Since CSR %, FO indices and species frequencies were obtained as proportions (ranged from 0 to 100 or from 0 to 1) we conducted beta-regressions to evaluate the relationship between CSR % and principal component axis, and also to evaluate the relationship between UNI and DIS, and between FO and species frequency. Beta-regressions were conducted using the logit link function and 'BFGS' algorithm for optimization, and to deal with the presence of 0 and 100 (or 1) in the dataset, we applied the transformation: $x' = (x(N-1) + 0.5)/N$, where N is the sample size, and x is the CSR %, FO or frequency converted to a 0-1 scale (Cribari-Neto and Zeileis 2010). All analyses were performed in the R environment (R Core Team 2014), with $P < 0.05$. BHPMF, cluster analysis, median tests and beta-regressions were performed under the R-packages 'BHPMF', 'vegan', 'nparcomp', and 'betareg', respectively.

2.1.4 Results

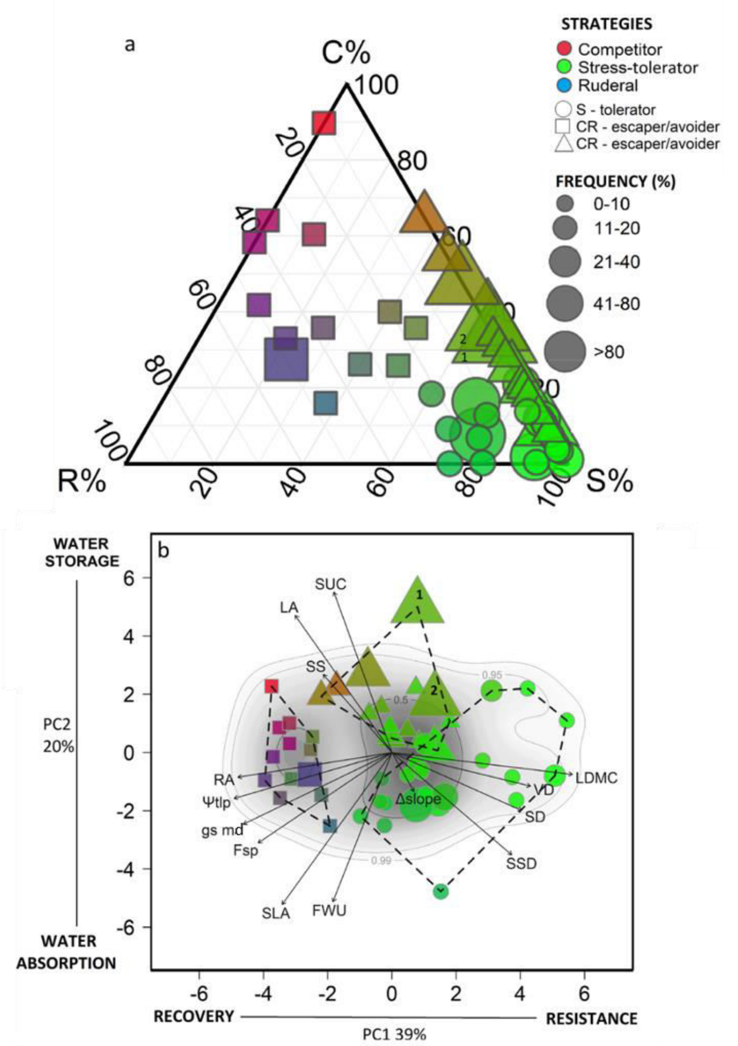
2.1.4.1 Eco-physiological strategies of response to drought

A large interspecific variability was found for most of the traits measured (Kruskall-Wallis test: $P < 0.01$), except for $g_{s\ md}$ ($\chi^2 = 11$; $P = 0.44$) and Δslope ($\chi^2 = 11$; $P = 0.43$). Regarding the CSR strategies, it was observed a predominance of stress-tolerator species (76 %), followed by competitor (14 %) and ruderals (10 %) (Fig. 2a). Three axes were retained from PCA (PC1-PC3), cumulatively explaining 73 % of the total variance (Fig. 2b). Economic, hydraulic and regenerative traits co-varied across those three axes, so that economic traits associated with a conservative strategy (higher LDMC and SSD) and hydraulic traits related to a greater tolerance to drought (higher SD and VD, more negative Ψ_{tlp}) clustered at the positive side of PC1. By contrast, hydraulic traits usually related to a lower tolerance (less negative Ψ_{tlp}) and higher regeneration by resprout (higher RA) were loaded at the negative side of PC1. Therefore, PC1 might represent a trade-off between resistance (higher PC1 scores) and recovery (lower PC1). Traits associated with greater leaf succulence (higher SUC and LA) clustered on the positive side of PC2, whereas, traits associated with greater ability for foliar water uptake (higher FWU) were located at the negative side of PC2, thus indicating a trade-off between water-storage (SUC) and water-absorption (FWU). Larger seed sizes (higher SS) were loaded at the positive side of the PC3, while a more isohydric behaviour (higher Δslope) was loaded at the negative side (Fig. S1). Cluster analysis separated species into three groups (Fig. 2b): group 1 (S-tolerator; n= 22) was composed of both shrubs and herbs species that showed traits associated with a conservative resource-use strategy (smaller SLA, higher LDMC) and a higher tolerance to drought (higher SSD, more negative Ψ_{tlp}). Species in this group also showed lower resprout ability (lower RA); group 2 (CR-escaper/avoider; n = 13) was exclusively represented by herbaceous species that exhibited a more acquisitive resource-use strategy (smaller SLA and lower LDMC), a potentially lower safety margin for losing turgor (higher $g_{s\ md}$, less negative Ψ_{tlp}), and a higher ability for foliar water uptake (higher FWU), and for resprouting (higher RA); and group 3 (CS-escaper/avoider; n= 16) was composed of herbs and shrubs with more succulent leaves (higher SUC), with larger leaves and seeds (higher LA and SS), and an intermediate position between conservative and acquisitive strategies.

There were significant differences among those three groups in terms of CSR strategies (Kruskall-Wallis test: $P < 0.01$; Figs 1a, S2). Group 1 was mainly composed of stress-tolerator species (higher S %), group 2 encompassed both ruderal and competitor species (higher R % or C %), while group 3 was composed of C/S species (higher C % and R %). PC1 was negatively associated with C % (Beta-regression: pseudo-R² = 0.47, $P < 0.01$,

Fig. S3a) and R % (pseudo-$R^2 = 0.43$, $P < 0.01$; Fig. S3c) and positively associated with S % (pseudo-$R^2 = 0.47$, $P < 0.01$; Fig. S3b). PC2 was positively associated with C % (pseudo-$R^2 = 0.32$, $P < 0.01$; Fig. S3d), negatively with R % (pseudo-$R^2 = 0.29$, $P < 0.01$; Fig. S3f), but not associated with S % (pseudo-$R^2 = 0.02$, $P = 0.04$; Fig. S3e), and no significant relationships were found between CSR % and PC3 (C%: pseudo-$R^2 = 0.01$, $P = 0.98$; S %: pseudo-$R^2 = 0.01$, $P = 0.38$; R %: pseudo-$R^2 = 0.01$, $P = 0.10$).

Figure 2 - Eco-physiological strategies of 51 plant speciesfrom a tropical mountain grassland (Itatiaia, RJ, Brazil).



Subtitle: (a) - CSR strategies (competitiveness, C%; stress-tolerance, S%; ruderalism, R%); (b) -trait loadings (vectors) and scores (points) along principal component analysis axes 1 (PC1) and 2 (PC2). Polygons delimit the three eco-physiological strategies(S- tolerator; CR- escaper/avoider, CS- escaper/avoider). Point shapes correspond to the eco-physiological strategies; point sizes represent the species frequency (%); and point colours were obtained by converting CSR % into red, green, and blue, respectively.

Numbers indicate the positions of the two-codominant species in the CSR triangle and in the functional space (PCA): 1. *Machaerina ensifolia* and 2. *Cortaderia modesta*. For traits abbreviations see Table 1.
Source: The author, 2019.

2.1.4.2 Functional originality and species loss scenarios

Chusquea pinifolia (UNI and DIS =1) was the most original species, followed by the dominant *M. ensifolia* (UNI = 0.86, DIS = 0.77) (Table S1). The co-dominant *C. modesta* exhibited relatively high uniqueness (UNI = 0.62), but low distinctiveness (DIS = 0.49). Conversely, the less unique species were *Sisyrinchium alatum* and *Lepechinia speciosa* (both UNI = 0.14), and the less distinct species belonged to the *Baccharis* genus, which was the most diverse genus in the studied area, with 11 species. A positive relationship was found between UNI and DIS considering all species together (Beta-regression: pseudo-$R^2 = 0.50$, $P < 0.01$; Fig S4), as well as, for S-tolerator (pseudo-$R^2 = 0.64$, $P < 0.01$) and CS-escaper/avoider (pseudo-$R^2 = 0.67$, $P < 0.01$), but not for CR-escaper/avoider species (pseudo-$R^2 = 0.19$, $P = 0.08$). Species frequency was not related to DIS (Beta-regression: pseudo-$R^2 = 0.03$, $P = 0.21$; Fig. S5b), and was positively associated with UNI (pseudo-$R^2 = 0.13$, $P < 0.01$; Fig. S5a), but this relationship was largely influenced by the two co-dominant species, that exhibited relatively high UNI values. Thus, when those two species were excluded from the analysis, the positive relationship vanished (pseudo-$R^2 = 0.02$, $P = 0.34$). UNI was evenly distributed across the three strategies (Kruskall-Wallis test: $\chi^2 = 2.89$, $P = 0.24$; Fig. 3a), whereas DIS was slightly higher for the CR-escapers/avoiders ($\chi^2 = 8.09$, $P = 0.02$; Fig. 3b).

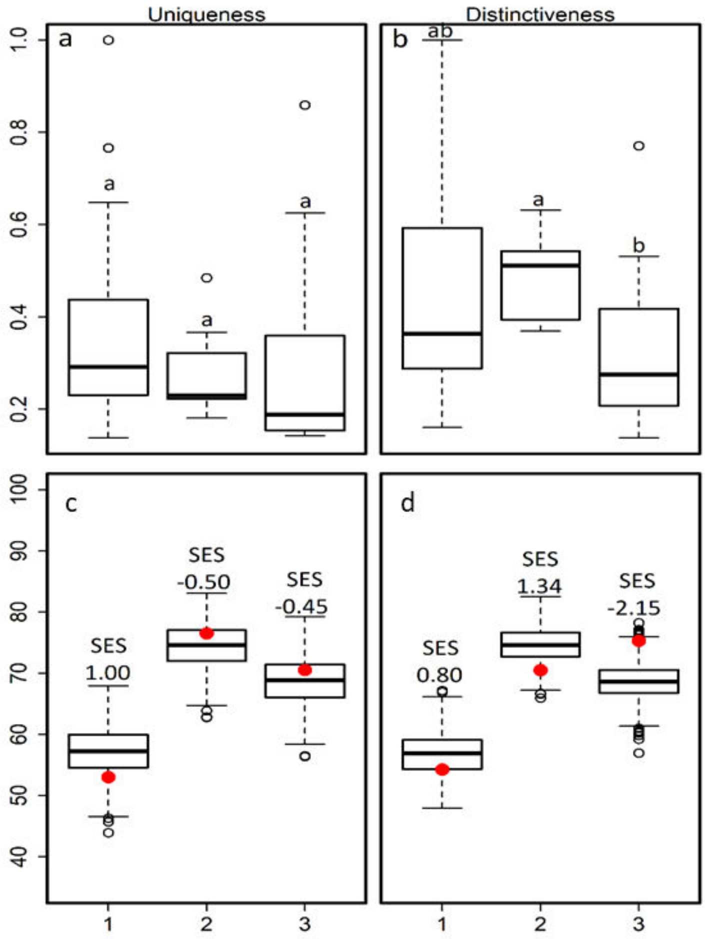
When compared to the random scenario of species loss, losing all S-tolerator species resulted in a greater loss of UNI (see the red point below the boxplot mean, Fig. 3c), while losing all R-escapers resulted in a greater loss of DIS (Fig. 3d). Counterwise, losing all CS-species resulted in a higher stability for both originality indices (Fig. 3c-d).

2.1.5 Discussion

2.1.5.1 Three eco-physiological strategies of response to drought

In the tropical mountain grassland studied, economic, hydraulic, and regenerative plant traits did not vary independently, but they were coupled in three distinct eco-physiological strategies: S-tolerator, CR-escaper/avoider and CS-escaper/avoider (Fig. 2).

Figure 3 - Functional originality indices of 51 plant speciesfrom a tropical mountain grassland (Itatiaia, RJ, Brazil).



Subtitle: distribution of functional (a) uniqueness and (b) distinctiveness across the three eco-physiological strategies in response to drought (1. S- tolerator; 2. CR- escaper/avoider, 3. CS- escaper/avoider) identified by cluster analysis for 51 grassland plant species. Letter codes indicate significant differences according to Kruskall-Wallis, followed by median tests; (c) and (d) -red points indicate the percentage of reduction in the community functional originality after the exclusion of all species whithin each of the three distinct strategies. Boxplots represent the mean and standard deviation for 1, 000 random simulations of species loss. SES represent the standardized effect sizes comparing random versus strategy scenarios of species loss. Positive SES values (and red points below the boxplot) indicate that losing all species from that specific strategy will resulted in a higher loss of functional originality than losing the same number of species randomly.

Source: The author, 2019.

The majority of species in this community were classified as S-tolerators, showing higher values of stress-tolerance in the CSR triangle (Fig. S2) and hence ‘slow’ economic traits, such as small LA, low SLA, and high LDMC and SSD. Those ‘slow’ traits seemed to simultaneously promote a conservative use of carbon and water resources, and a higher tolerance to dehydration (Villagra et al. 2013, Reich 2014). The smaller leaves of the S-tolerator species, for example, might be a result of their slow-growth rates, but might also be a mechanism for reducing water loss by transpiration during drought (Markesteijn and Poorter 2009). In the same way, higher SSD is commonly associated with lignified and mechanically strong tissues, and hence, it is likely to support a lower xylem vulnerability to cavitation (Pockman et al. 2001, Santiago et al. 2018), thus allowing those conservative species to maintain turgor and hence their physiological activities under more negative water potentials (Reich 2014). Moreover, the higher densities of both stomata and leaf veins (higher SD and VD) found in this group suggest a coordination between water demand (SD) and water supply (VD) and are also typically associated with a higher drought tolerance (Sack and Scoffoni 2013). A higher VD can promote dehydration tolerance by conferring higher redundancy in the water transport system, and thus enabling a continued water flux despite the embolism of some veins (Sack and Scoffoni 2013, Sack and Holbrook 2006), whereas a higher SD may help the S-tolerator species to reduce transpiration by a quicker onset of stomatal regulation when water becomes scarce (Xu and Zhou 2008). Stomatal regulation can occur not only by controlling the density of stomata but also the degree of stomatal pore aperture (i.e. stomatal conductance). Besides a higher SD, S-tolerator species also exhibited relatively lower g_{smd}, which is consistent with their conservative strategy and might be associated to their isohydric behaviour (higher Δslope).

Contrarily to the theoretical expectations, we did not find a clear separation between R-escapers and C-avoiders species (Fig. 1). The other two eco-physiological groups represented a combination of those strategies. Thus, CR-escapers/avoiders included both ruderal herbs and some competitor species (*L. tweediei*, *Senecio oleosus*, *Trixis glaziovii*, and *Plantago australis*); while the CS-escapers/avoiders was composed by species occupying intermediate positions along the CS axis (competitor – stress-tolerant axis). Besides, both groups could either escape or avoid dehydration, although by using different mechanisms.

CR-escapers/avoiders appeared not to be able to down-regulate water-use (higher g_{smd}) under increasing atmospheric waterdeficit stress, thus they would be more prone to lose turgor given their higher Ψ_{tlp}. A higher ability to perform foliar water uptake (higher FWU) could compensate this trend (Limm et al. 2009) and be an avoidance mechanism to maintain leaf hydration when the soils are dry but the atmosphere is humid, such during fog events. However, if soil and atmospheric droughts co-occur, CR-escapers/avoiders might not be able to avoid dehydration. In this case, those species could still rely on escaping strategies, returning to the community after drought alleviation via regeneration (higher RA). CS species, in turn, seemed to avoid drought by storing water, given their more succulent leaves (high SUC). The avoidance through succulence required then a combination of stress-tolerance characteristics, such as a conservative resource-use (low SLA) with a preferential allocation to storage rather than to growth (Wilson and Lee 2000, Pierce et al. 2013); and competitor characteristics, such as low LDMC and larger LA, which would allow greater water storage. As result, those species occupy intermediate positions along the 'fast-slow' spectrum, as well as, along the C-S triangle axis. Although CS species were more succulent when compared to the other strategies, their SUC values (mean = 2.69 H_2O dm^{-2}, range = 1.97 to 5.27 H_2O dm^{-2}) were mostly lower than 5 g H_2O dm^{-2}, which is the threshold value to consider a species as succulent (Pierce et al. 2013). According to Camerik and Werger (1981), the presence of highly succulent leaves could be unfavourable in a cold-mountainous environment, since succulent leaves would be far more liable to frost damage. Therefore, the amount of water stored by CS-escapers/avoiders species might be able to maintain their leaf turgor and gas exchange during mild, short and infrequent droughts, but is likely to be depleted under severe, long and frequent droughts. CS-species also exhibited the lower ability for foliar water uptake (lower FWU), thus corroborating the existence of a trade-off between water-storage (SUC) and water-absorption (FWU) (PC2 in the Fig. 2b), as suggested in previous studies (Gotsch et al. 2014).

Regarding the regeneration traits, CS-species invested in the production of larger seeds (larger SS), that could result in higher rates of seedling establishment after drought (Leishman and Westoby 1994, Khurana et al. 2006), while CR-species showed a higher resprout ability (higher RA), which may enable those species to recover their above-ground biomass following drought alleviation (Pausas et al. 2015). Contrarily, S-tolerator species showed lower RA and produced smaller seeds. Those results might suggest the existence of a trade-off between tolerance and regeneration (i.e. resistance and recovery), which can be observed along the PC1 (Fig. 2b). As hypothesized by the CSR theory (Grime 2001, Grime and Pierce 2012), C and R species (located at the negative side of the PC1) might be easy to damage, because they lack the hydraulic traits to tolerate drought, but their acquisitive strategy would favor a faster regeneration either by resprouting or by producing larger; while the S species (located at the positive side of the PC1) might be more drought tolerant, but once their tolerance threshold was exceeded and they were damaged, their conservative strategy (slow vegetative and reproductive growths) would impose a slower regeneration(Grime and Pierce 2012, Pausas et al. 2015). Nonetheless, more studies specifically testing this trade-off are still necessary, since there is also evidence that tolerance and regeneration could be positively associated at the individual level, if the conservative strategy of the stress-tolerator species would provide larger amounts of stored resources available for resprouting after the drought alleviation (Zeppel et al. 2014). Furthermore, the smaller seeds of stress-tolerator species could remain viable in the seed bank for longer periods, thus promoting regeneration by seedling as well (Pake and Venable 1996).

2.1.5.2 Community vulnerability to functional homogenization

In summary, when compared to a scenario where the same number of species were extinct randomly, losing all S-tolerator species had a greater impact on the functional uniqueness (UNI); losing all CR-species affected functional distinctiveness (DIS); while the loss of CS-species had no relevant impactson originality indices (Fig. 3).Although some S-tolerator species overlapped in the functional space, especially those located near the center (Fig. 2b), other species in this group, such as *C. pinifolia* and *C. capitata*, were more isolated, not sharing their combination of traits with neighbouring species, and thus showing higher UNI (Table S1). Consequently, losing all species in this strategy resulted in a decrease in the community UNI slightly greater, when compared to the random scenario (Fig. 3c).

The extinction of all CR-escapers/avoiders led to a greater loss of DIS (Fig. 3e) because, in average, species in this strategy were located further from the center of the functional space (Fig. 2b), thus exhibiting a trait-combination that differed from the mean values of the community. Conversely, losing all the species in the CS-escape/avoidance strategy resulted in a lower vulnerability to functional homogenization (Fig. 3 c-d), because species in this strategy were located closer to the center of the functional space and overlapped among them and even with some S-tolerator species (Fig. 2b), thus showing lower originality values (Fig. 3 a-b).

Interestingly, the two co-dominant species exhibited the same CS strategy (Fig. 2a) but differed in their originality values. *M. ensifolia* was more unique and distinct than *C. modesta*, probably because the former species exhibited LA and SUC values much higher when compared to the other species (Table S1). In fact, no relationship was found between species frequency and functional originality, thus both rare and dominant species could be either original or redundant (Fig. S6). Similarly, species with different CSR strategies exhibited distinct values of originality.

Finally, as reported in previous studies (e.g. Grenié et al. 2017), a positive association was found between UNI and DIS, particularly for the S-tolerator and CS-escaper/avoiders (Fig. S4). If those indices were not related to each other, then the extinction of a highly distinct species not mandatorily would result in functional homogenization, since a highly distinct, but not unique species, would share their distinct traits with other coexisting species (Mouillot et al. 2013). However, once these two indices are positively associated, highly distinct species would also be highly unique, and their loss would result in greater impacts on the community functioning. Therefore, to avoid the loss of functional diversity, the simultaneously distinct and unique species, such as the S-tolerators *C. pinifolia* and *C. capitata*; the CR-escapers/avoiders: *H. lutea*, *L. tweediei*; and the CS-escapers/avoiders: *M. ensifolia* and *C. modesta*, should receive more attention for conservation (Pavoine et al. 2005).

2.1.6 Conclusions

Based on a set of economic, hydraulic and regenerative traits, we classified species from a tropical mountain grassland in three distinct plant eco-physiological strategies: S-tolerator, CR-escaper/avoider and CS-escape/avoider, which we expect to respond differently under distinct scenarios of drought.

Under moderate, long-term and/or frequent droughts, S-tolerator are expected to resist, as they possess a conservative water use strategy and hydraulic traits that enable them to maintain their physiological activities as the water potential decreases (Villagra et al. 2013, Reich 2014). CS-escaper/avoiders, however, could succumb since longer and/or more frequent droughts would be likely to induce a depletion of the water stored. As recovery can only occur if periods of drought are followed by sufficient precipitation (Ruppert et al. 2015), longer and/or more frequent droughts could also lead to the extinction of CR species, especially if dryer soils conditions were associated with reduced leaf-wetting events, thus preventing those species to perform foliar water uptake. Although the loss of CS-escape/avoiders could not have immediate effectson community originality levels (due to its lower originality/higher redundancy), the loss of CR-escapers/avoiders, would cause a greater impact on the community functional distinctiveness. At the other hand, intense, short-term and infrequent droughts would be a disturbance for both CS and CR species, thus inducing loss of biomass. Despite their lower resistance, those species would be more likely to recover either by seeding or resprouting. Conversely, if more intense droughts surpassed the resistance thresholds of S-tolerators species, causing severe damages, those species would recover very slowly or even would be unable to recover (Grime and Pierce 2012). If S-tolerators went extinct then there would be a greater loss of community functional originality, especially in terms of uniqueness.

As more reliable trait gap-filling methods (Taugourdeau et al. 2014, Schrodt et al. 2015) and less labour-intensive trait measurement techniques (Bartlett et al. 2012, Brodribb et al. 2016) are being developed, it is becoming viable to obtain economic, hydraulic and regenerative traits for a larger number of co-existing species (Brodribb 2017, Griffin-Nolan et al. 2018) and then to use the framework proposed here, integrating eco-physiological strategies and functional originality indices, for predicting species and community vulnerabilities to functional impairment in response to droughts.

2.1.7 Acknowledgments

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2.1.9 Supporting information

Figure S1 **-** Results of principal component analysis (PCA) for 14 economic, hydraulic and regenerative traits and 51 species from a tropical mountain grassland (Itatiaia, RJ, Brazil).

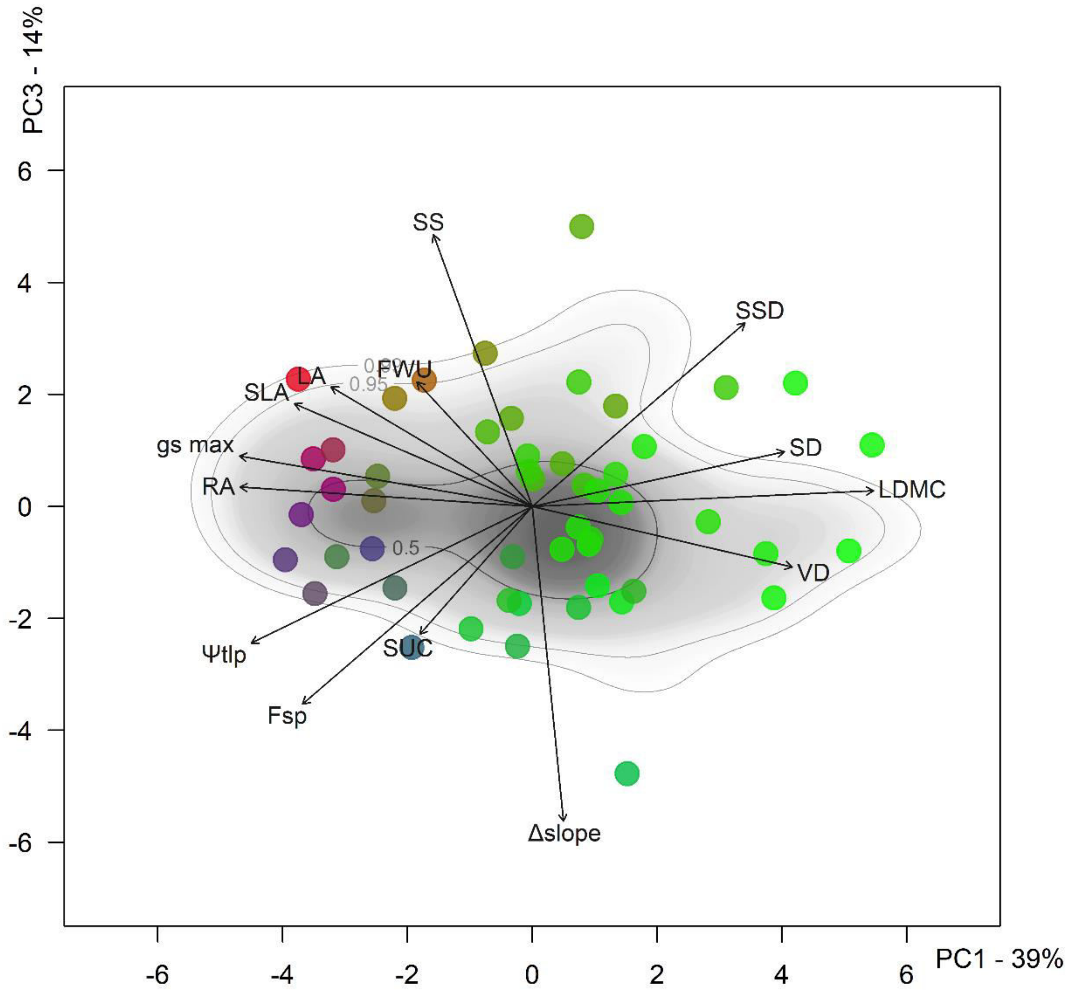
Figure S2 - Distribution of CSR ecological strategies across the three eco-physiological strategies defined by clustering analysis.

Figure S3 - Results of beta-regression among principal component analysis axes 1 (PC1) and 2 (PC2), and the CSR ecological strategies (competitiveness, C %; stress-tolerance, S %; ruderalism, R %) for 51 species from a tropical mountain grassland (Itatiaia, RJ, Brazil).

Figure S4 - Results of beta-regression between uniqueness and distinctiveness for 51 species from a tropical mountain grassland (Itatiaia, RJ, Brazil).

Figure S5 - Results of beta-regression between species frequency and functional originality indices (uniqueness and distinctiveness) for 51 species from a tropical mountain grassland (Itatiaia, RJ, Brazil).

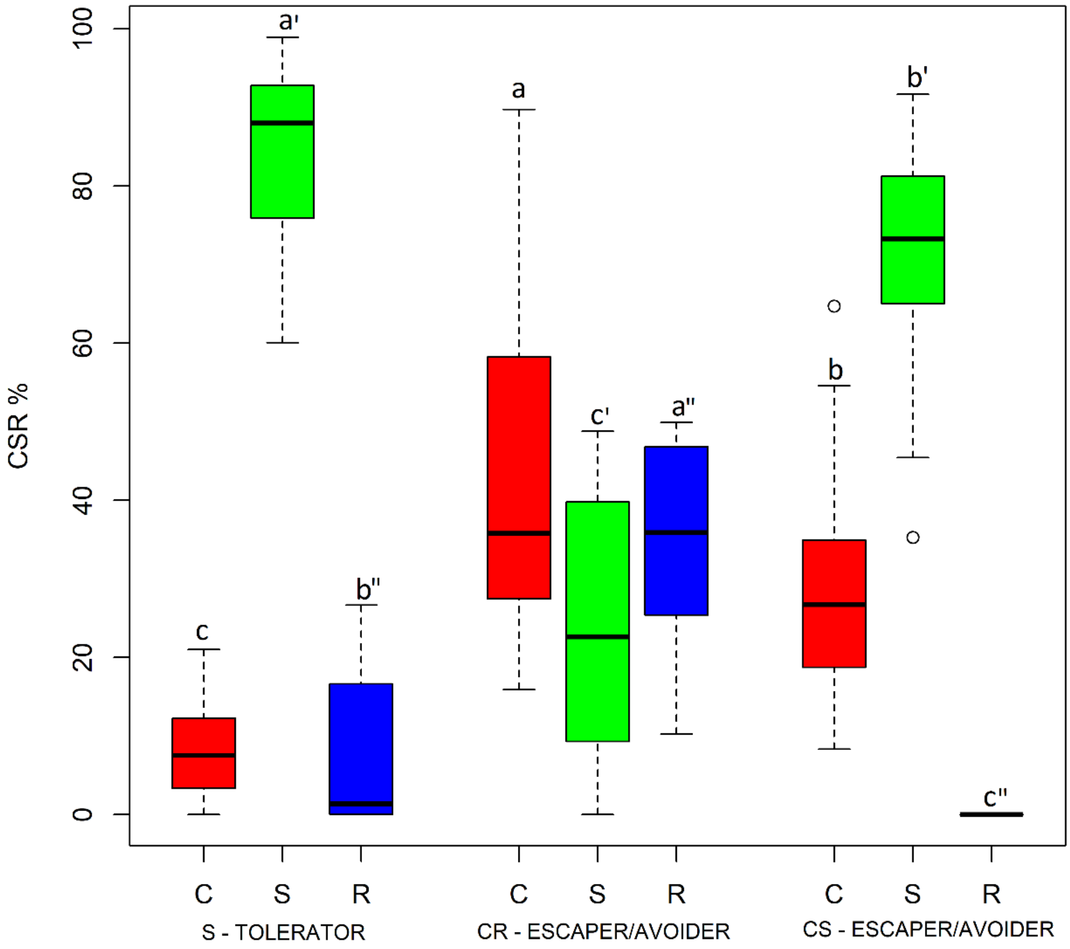
Figure S1 - Results of principal component analysis (PCA) for 14 economic, hydraulic and regenerative traits and 51 species from a tropical mountain grassland (Itatiaia, RJ, Brazil).



Subtitle: trait loadings (vectors) and scores (points) for 51 grassland plant species along principal component analysis axes 1 (PC1) and 3 (PC1). Point colours were obtained by converting CSR % into red (competitiveness), green (stress-tolerance), and blue (ruderalism). For traits abbreviations see Table 1.

Source: The author, 2019.

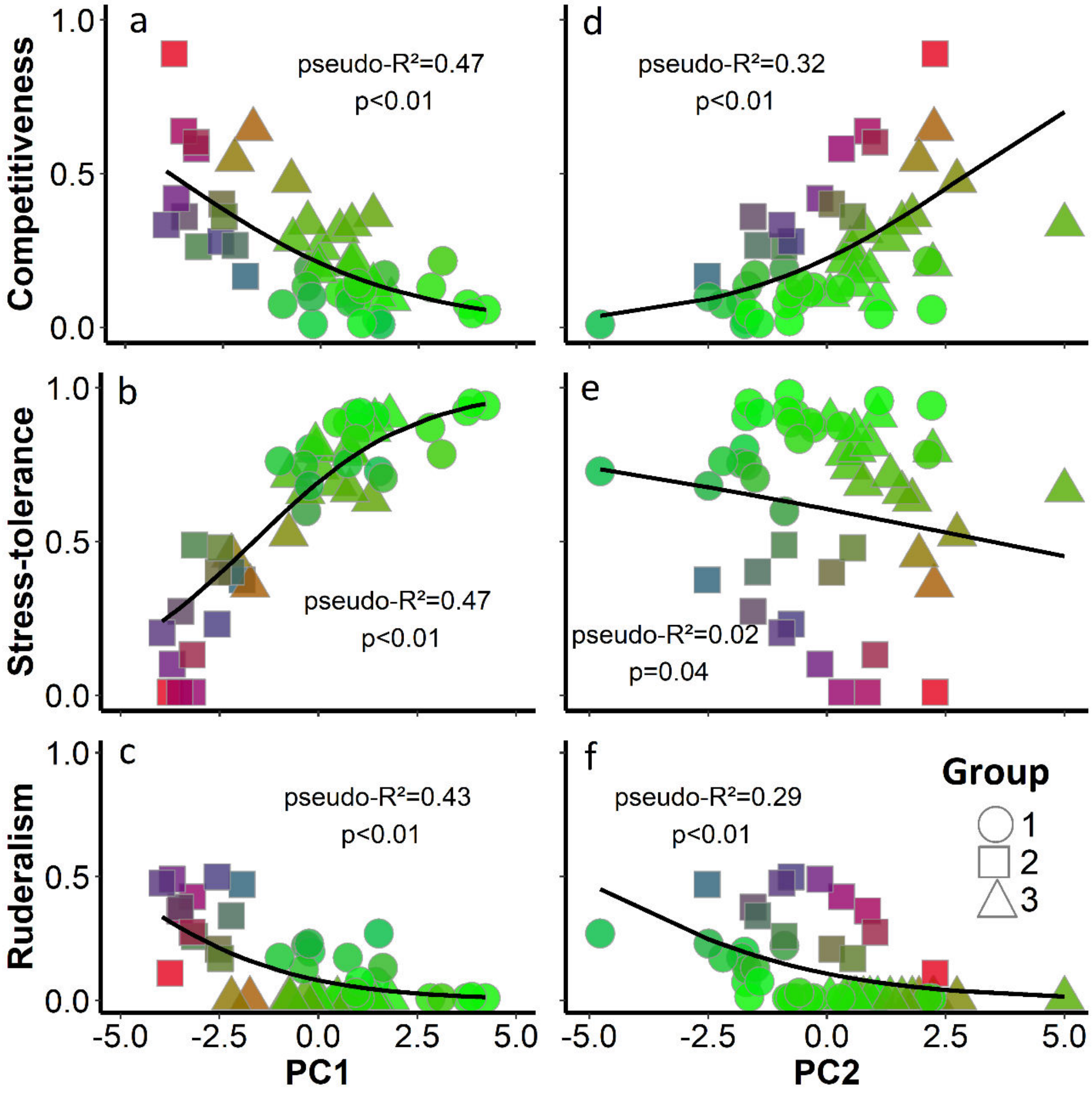
Figure S2 - Distribution of CSR ecological strategies across the three eco-physiological strategies defined by clustering analysis.



Subtitle: CSR ecological strategies (competitiveness, C%; stress-tolerance, S%; ruderalism, R%); eco-physiological strategies (S- tolerator; CR- escaper/avoider, CS- escaper/avoider). Letter codes indicate significant differences for each CSR % across the three strategies according to Kruskall-Wallis, followed by median tests.

Source: The author, 2019.

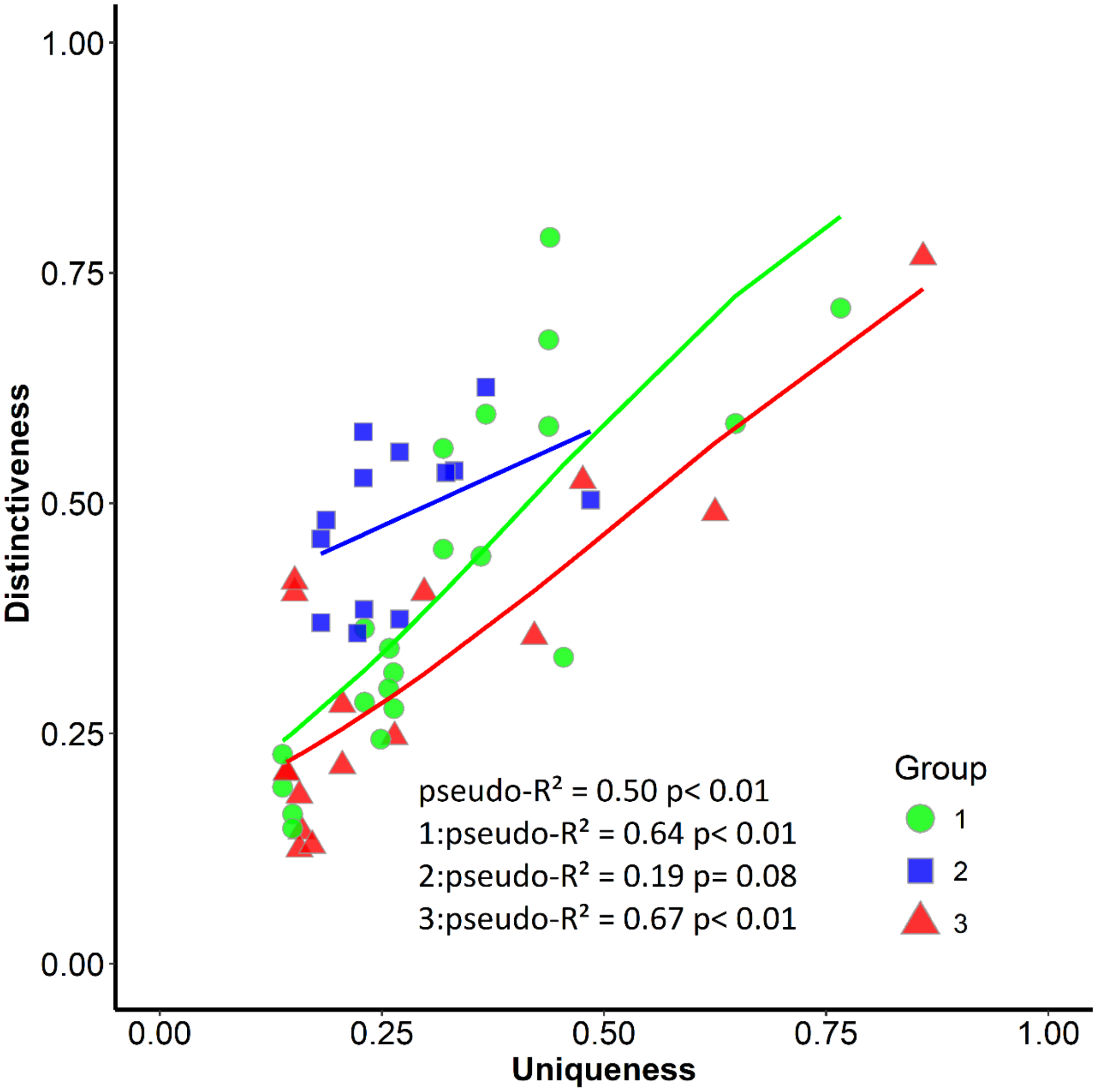
Figure S3 - Results of beta-regression among principal component analysis axes 1 (PC1) and 2 (PC2), and the CSR ecological strategies (competitiveness, C%; stress-tolerance, S%; ruderalism, R%) for 51 species from a tropical mountain grassland (Itatiaia, RJ, Brazil).



Subtitle:point colours were obtained by converting CSR % into red, green, and blue, respectively and point shapes represent the three eco-physiological strategies (groups) of response to drought identified by cluster analysis(1. S- tolerator; 2. CR- escaper/avoider, 3. CS- escaper/avoider).

Source: The author, 2019.

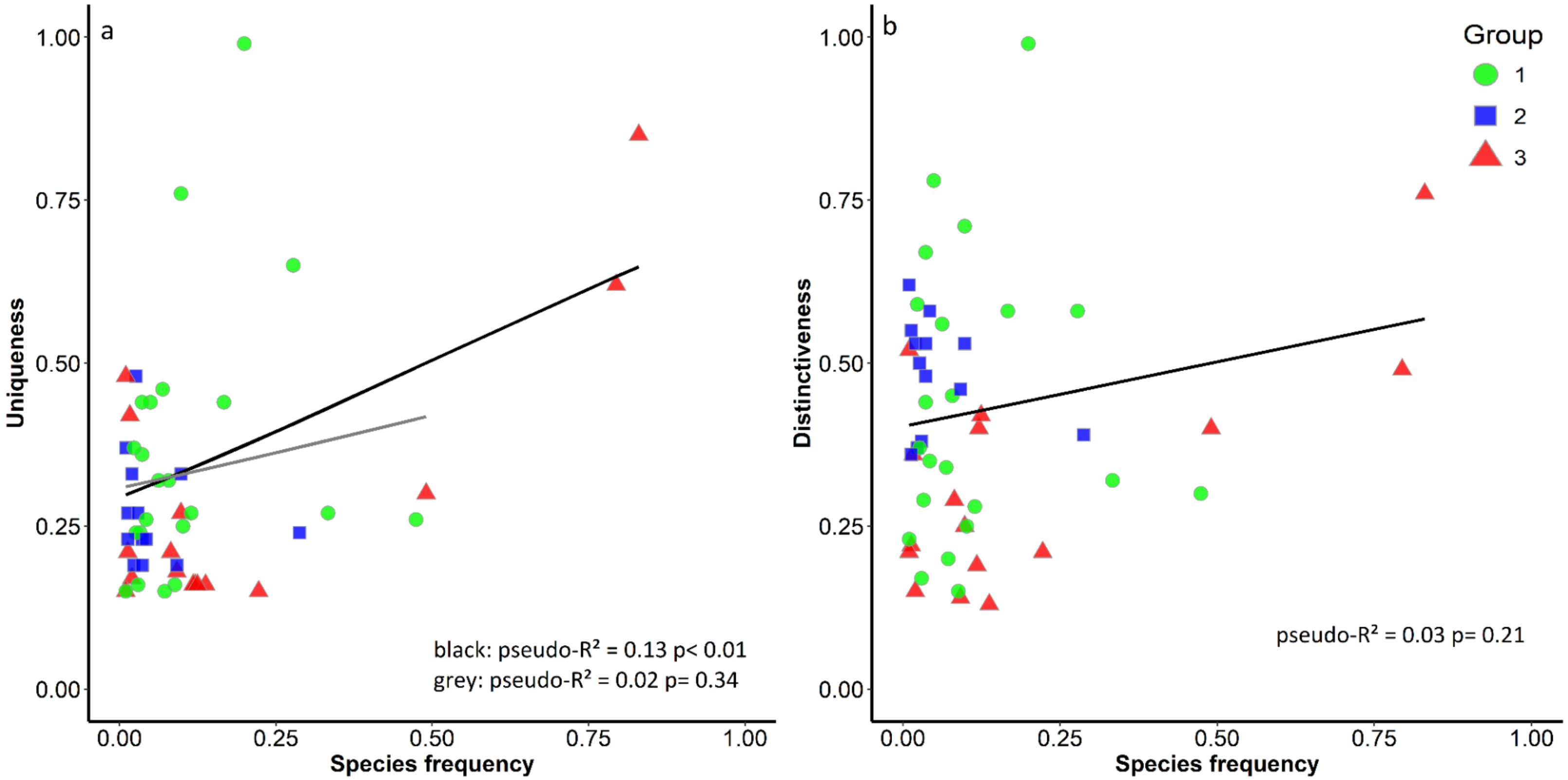
Figure S4 - Results of beta-regression between uniqueness and distinctiveness for 51 species from a tropical mountain grassland (Itatiaia, RJ, Brazil).



Subtitle: point shapes and colors indicate the three eco-physiological strategies (groups) of response to drought identified by cluster analysis (1. S- tolerator; 2. CR- escaper/avoider, 3. CS- escaper/avoider).

Source: The author, 2019.

Figure S5 - Results of beta-regression between species frequency and functional originality indices (uniqueness and distinctiveness) for 51 species from a tropical mountain grassland (Itatiaia, RJ, Brazil).



Subtitle: point shapes and colors indicate the three eco-physiological strategies (groups) of response to drought (1. S- tolerator; 2. CR- escaper/avoider, 3. CS-escaper/avoider) identified by cluster analysis. In fig. a grey line was fitted after the exclusion of the two co-dominant species *M. ensifolia* and *C. modesta*.

Source: The author, 2019.

3 **O EFEITO DAS FONTES ALTERNATIVAS DE ÁGUA**

> It is better to know how to learn than to know
> *Dr. Seuss*

3.1 **Who are the leaf water uptakers? Determining leaf traits that influence atmospheric water absorption by plants**[1]

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Running headline: Functional and ecological implications of foliar water uptake

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[1] Author's Contributions: ISM and BHPR conceived the idea and experiments. ISM and WFG performed the experiments and ISM, WFG, DGM, IO and BHPR analyzed and interpreted the data. ISM led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

3.1.1 Abstract

1. Plants can absorb atmospheric sources of water, such as fog, to maintain their water status, a phenomenon called foliar water uptake (FWU). With the increased occurrence of extreme droughts, FWU could be an ecological advantage by increasing a plant ability to cope with soil water shortages. However, the frequency of leaf-wetting events, is also predicted to decrease, especially in mountainous environments. Although previous studies have shown that species largely differ in FWU, there is little information on how those differences are associated with plant functional traits and ecological strategies. Therefore, we are uncertain about how changes in both soil and atmospheric water availabilities would affect plant communities.
2. In this study, anatomical, morphological and physiological leaf traits were measured on 76 species from a tropical mountain grassland, and we determined which traits and ecological strategies (competitive, stress-tolerator, and ruderal; CSR) were related to greater FWU.
3. Increases in FWU were associated with increases in the ruderal strategy and with higher specific leaf area and stomatal conductances, but lower leaf dry matter content, succulence, and thickness. On the other hand, stress-tolerator species exhibited less FWU. Contrarily to previous studies, FWU was not correlated with leaf wettability, leaf water potential at the turgor loss point nor with iso-/anisohydric behaviour.
4. We concluded that more ruderal species are the main leaf water uptakers. Therefore, plant communities dominated by ruderals might be more dependent on leaf-wetting events to maintain water balance, and hence would be more greatly affected by reductions in fog occurrence.

Key-words: iso-/anisohydric behaviour, CSR theory, drought resistance, leaf wettability, *Campos de Altitude.*

3.1.2 Introduction

In recent years, many studies have focused on identifying the plant traits that may indicate a species ability to cope with drought (Blackman et al. 2010, Choat et al. 2012). Notwithstanding the great advances in trait-based approaches, the criteria for selecting functional traits that describe a given process remain a matter of debate in the literature (Funk et al. 2016, Rosado and de Mattos 2017). Within this context, foliar water uptake (FWU) has emerged as an important trait associated with improvements in plant functioning during drought across several species and environments (Oliveira et al. 2014, Goldsmith et al. 2012). FWU can increase leaf water potential, photosynthetic rates, and stomatal conductance

(Burgess and Dawson 2004, Eller et al. 2013), resulting in long-term benefits, such as recovery from xylem cavitation (Gouvra and Grammatikopoulos 2003), improving plant growth (Boucher, Munson, & Bernier, 1995), and extending plant life-time (Vaadia and Waisel 1963).

Despite these benefits, not all species within a community can perform FWU equally (Fu et al. 2015, Goldsmith et al. 2012, Limm et al. 2009). Interspecific variability in FWU may be related to species life-form and phenology (Fu et al. 2015), and to leaf traits, such as leaf water potential (Ψ_{leaf}, Breshears et al. 2008), leaf water potential at the turgor loss point (Ψ_{tlp}, Gotsch et al. 2015), stomatal conductance (g_s, Berry et al. 2014), and iso-/anisohydric behaviour (Eller et al. 2016). Although previous studies have indicated some traits that potentially influence FWU, we still lack a community-wide and multiple-trait evaluation of proxies for FWU. Furthermore, since plants in a community can cope with drought via different combinations of traits (Pivovaroff et al. 2016), it is also important to investigate the interplay between FWU and plant ecophysiological strategies. As reported by Gotsch et al. (2015), in a study of 11 epiphytes and hemiepiphytes from a tropical montane cloud forest, trade-offs might exist between traits conferring drought tolerance and FWU (i.e. more negative Ψ_{tlp} resulted in greater FWU) versus traits conferring leaf capacitance and drought avoidance (i.e. greater leaf thickness and succulence resulted in less FWU; Gotsch et al. 2015).

In terms of ecological strategies, the CSR theory (Grime 1977) is one of the most empirically supported schemes (Pierce et al. 2017). According to this theory, there is a triple trade-off between a speciesability to compete with its neighbours (competitor, C), to resist stresses (stress-tolerators, S), and to cope with disturbance (ruderal, R). Therefore, plant species exhibit different proportions of each of those three primary strategies. C-strategists are large, fast-growing organisms, with large leaves (large leaf area, LA) and an acquisitive leaf economic strategy. That is, they exhibt large specific leaf area (SLA) and low leaf dry matter content (LDMC), which are characteristics that maximise the capture of resources and vegetative growth in resource-rich and undisturbed conditions. S-strategists are short, slow-growing, long-living organisms, with small, dense, and tough leaves (e.g. small SLA and LA, high LDMC) and a conservative resource-use strategy. Their characteristics allows preservation of metabolic processes at the expense of both vegetative and reproductive growth in resource-poor habitats. Finally, the R strategy is characterised by organisms with short stature, short life-history, small and thin leaves (e.g. large SLA, low LDMC and small LA), which invest mainly in reproductive growth and occur in severely disturbed, but potentially resource-rich environments (Grime 1977, Pierce et al. 2017).

Under the CSR perspective, if FWU is a mechanism that improves drought resistance (Limm et al. 2009, Yang et al. 2010), one would expect S species to exhibit higher FWU and experience advantages under future drier conditions. Alternatively, recent findings have suggested that tree species with high FWU exhibit anisohydric behaviour and could be more prone to foliar turgor loss (Eller et al. 2016). Thus, it is still necessary to elucidate how FWU may affect tolerance to/avoidance of drought. A better understanding of FWU and how it interacts with other leaf traits and plant ecological strategies would improve our understanding of the morpho-physiological mechanisms underlying this process, and would be especially relevant in the context of climate change, during which reductions in both precipitation and fog events are expected (Pounds et al. 1999, Zhang et al. 2007).

In this study, we selected 76 species (grasses, forbs, and shrubs) from a fog-occurring environment, the Brazilian *Campos de Altitude*, and measured their FWU as well as a set of anatomical, morphological, and physiological leaf traits to answer the following questions:

1) At what extent co-occurring species differ in the quantity of water absorbed by their leaves?
2) Is there an association between FWU and plant CSR strategies?
3) Which leaf traits are related to greater FWU?

Our first hypothesis (H1) is that, given the high frequency of fog events in the evaluated community, all species will perform FWU, but there would be significant interspecific differences in the amount of water absorbed. Our second hypothesis (H2) is that the interspecific variability in FWU would be associated with CSR strategies; thus, FWU would be positively associated with stress-tolerance (Gotsch et al. 2015), but negatively associated with competitiveness and ruderalism. Consequently, we hypothesise (H3) that traits known to provide higher drought tolerance (e.g. small SLA, high LDMC, low leaf water potential) would be associated with higher FWU.

This is the first study addressing FWU, an important aspect of ecophysiological functioning, in *Campos de Altitude*, which is one of the most important neotropical montane ecosystems (Aparecido et al. 2018).

3.1.3 Materials and methods

3.1.3.1 Study area

This study was conducted at the *Campos de Altitude* in the Itatiaia National Park (INP) in Southeast Brazil (22º22'37" S, 44º42'28" W, above 2, 400 m asl). The vegetation is composed of shrubs and stunted trees that are sparsely distributed in a herbaceous matrix (Giovanetti-Alves 2013). The climate is typical of a tropical altitude (Cwb - Köppen), with mean minimum and maximum annual temperatures of 7.4°C and 13.6°C, respectively (Safford 1999). The mean annual precipitation is about 2, 200 mm, with a three-month dry season in the winter (Jun-Aug). Dry spells can occur during the wet season (Dec-Feb), especially in the El Niño years (Safford 1999). Fog occurs on 65–90% of days per year (Segadas-Vianna and Dau 1965).

We sampled76 species, comprising 84.8% of the cumulative species frequency (see Appendix S1), including different life-forms (grasses, forbs, and shrubs) and dominances (rare and dominant). Species were sampled to determine FWU, CSR strategies, and anatomical, morphological and physiological leaf traits (Table 1).

3.1.3.2 Foliar water uptake

FWU was determined following the methods of Limm et al. (2009). For each species, five branches (five whole individuals for herbs) were sampled, placed between damp sheets of paper, and rehydrated for 72 h at 5 °C in the darkness.

Table 1- List of morphological, anatomical and physiological leaf traits and foliar water uptake measurements.

Leaf trait	Abbreviation/Symbol
Anatomical	
Stomatal density	SD
Average fraction of the leaf surface allocated to stomatal pores	Fsp
Average fraction of the leaf surface allocated to guard cells	Fgc
Morphological	
Leaf area	LA
Leaf dry matter content	LDMC
Leaf succulence	SUC
Leaf thickness	Lth
Leaf water hydrophobicity	LWH
Specific leaf area	SLA
Physiological	
Leaf water potential at the turgor loss point	Ψ_{tlp}
Minimum midday leaf water potential	Ψ_{min}
Mean midday leaf water potential	Ψ_{mean}
Pre-dawn leaf water potential	Ψ_{pd}
Maximum midday stomatal conductance	$g_{s\ md}$
Mean midday stomatal conductance	$g_{s\ mean}$
Leaf water potential when the stomatal conductance drops to 50% of the maximum stomatal conductance	$\Psi_{gs50\%}$
Degree of iso-/anisohydric behaviour	Δslope
Foliar water uptake	
Foliar water uptake flux	FWU_{flux}
Foliar water uptake leaf water content	FWU_{lwc}
Foliar water uptake return	FWU_{lwr}

Source: The author, 2019.

After rehydration, one mature healthy leaf per branch (or individual) was excised and its mass was determined (m_0). Next, the leaf was allowed to dry on a bench for 3 h at 20 °C, it was weighed (m_1) and submersed in distilled water in darkness for 3 h. Before submersion, the petiole was sealed with Vaseline to prevent water entry. Leaf submersion was used to standardise water availability across the morphologically diverse foliar types and represents the maximum quantity of water that a plant could absorb.

After 3 h of submersion, the leaf was dried with paper towels and the mass was recorded (m_2). To account for any potential errors associated with residual water on the leaf surface, the leaf was allowed to dry on the bench (about 5 min), after which the mass was recorded again (m_3). The leaf was re-submersed in water for 1 s, dried, and reweighed (m_4). This brief re-wetting did not allow sufficient time for water absorption, so any increase in mass represents the residual water on the leaf surface. All leaves were scanned to measure leaf area (LA) using the software Image J, version 1.48 (http://rsbweb.nih.gov/ij/), and were then dried at 50 °C for 96 h to determine the dry mass (m_{dry}).

The FWU flux ($\mathrm{FWU_{flux}}$, mg H_2O cm^{-2} $hour^{-1}$; Equation 1) was calculated as the difference between the leaf mass before (m_1) and after (m_2) submersion in water, corrected for residual water (m_4-m_3), standardised with one-sided LA, and divided by the submersion time (3 h):

$$\mathrm{FWU}_{flux} = \frac{\frac{(\mathrm{m2}-(\mathrm{m4}-\mathrm{m3})-\mathrm{m1})}{\mathrm{LA}}}{\mathrm{time}} \qquad (1)$$

To determine how the dehydration/rehydration cycle influenced leaf water content (lwc), FWU was also calculated as the percentage increase or decrease in the lwc ($\mathrm{FWU_{lwc}}$, %; Equation 2):

$$\mathrm{FWU}_{lwc} = \left[\frac{(m2-(m4-m3)-m_{dry})}{(m1-m_{dry})} - 1\right] * 100 \qquad (2)$$

Finally, to determine the percentage of water regained through FWU compared with full hydration (m_0), we computed the FWU return ($\mathrm{FWU_{lwr}}$, %: Equation 3). An $\mathrm{FWU_{lwr}} = 0$ indicates a complete return to initial hydration, negative values indicate a net loss of water, and positive values indicate a net gain:

$$\mathrm{FWU}_{lwr} = \left[\frac{(m2-(m4-m3)-m_{dry})}{(m0-m_{dry})} - 1\right] * 100 \qquad (3)$$

The FWU indices were obtained based on leaf mass measurements, representing absolute values over an unknown water potential gradient. Therefore, caution was needed when inferring the role of FWU in promoting leaf/xylem pressure alleviation during drought.

3.1.3.3 Leaf functional traits and CSR strategies

The morphological traits, that is, leaf thickness (Lth, mm), leaf area (LA, mm²), specific leaf area (SLA, $mm^2 mg^{-1}$), leaf dry matter content (LDMC, %), leaf succulence (SUC, $g m^{-2}$), and mean leaf water hydrophobicity (LWH, °), were measured in 10 individuals per species. Detailed methods are described in Appendix S1.

The CSR coordinates for each species were computed using the 'globally-calibrated CSR strategy calculator tool StrateFy'(Pierce et al. 2017). In StrateFy, the LDMC, SLA, and LA of each species were compared against the axes of a multivariate space occupied by 3, 068 tracheophytes, thus returning a relative percentage for the competitiveness (C%), stress-tolerance (S%), and ruderalism (R%) of each species (Pierce et al. 2017).

To evaluate the anato-physiological traits, we selected a subset of 12 species: *Achyrocline satureioides* (Lam.) DC.; *Baccharis uncinella* DC.; *Chionolaena capitate* (Baker) Freire; *Chusquea pinifolia* (Nees) Nees; *Cortaderia modesta* (Döll.) Hack; *Eryngium glaziovianum* Urb.; *Gamochaeta purpurea* (L.) Cabrera; *Hypochaeris lutea* (Vell.) Britton; *Leptostelma maximun* D. Don; *Machaerina ensifolia* (Boeckeler) T. Koyama; *Mikania glaziovii* Baker; and *Pleroma hospita* (Schrank et Mart. ex DC.) Triana. Selection was based on the following criteria: (i) the species represented the range of variations of CSR proportions in the evaluated community; (ii) the species leaves were large enough to allow such measurements; and (iii) the species was not a rare or ephemeral species.

For anatomical measurements, one leaf from five individuals per species was subjected to the diaphanisation technique (Strittmater 1973) and mounted on glass slides to obtain the stomatal density (SD, number mm^{-2}), the average fraction of the leaf surface allocated to guard cells (Fgc, %), and the average fraction of the leaf surface allocated to stomatal pores (Fsp, %).

In terms of physiological traits, predawn (Ψ_{pd}, MPa) and midday leaf water potential (Ψ_{md}, MPa) and midday stomatal conductance (g_{smd}, mmol m^{-2} s^{-1}) were measured monthly (from June -2016 to June -2017) in two individuals per species using a leaf porometer (model SC1, Decagon Devices, Pullman, WA, USA) and a Scholander chamber (model 1505D-EXP, PMS, Albany, OR, USA), respectively. We computed the mean (g_{smean}) and maximum midday stomatal conductance ($g_{s\ md}$) and the mean (Ψ_{mean}) and minimum midday leaf water potential (Ψ_{min}). We also used those data to determine the two indices of iso-/anisohydric behaviour: (i) Δslope, that is, the slope of a linear regression fitted to a plot of log (Ψ_{pd}-Ψ_{md}) versus Ψ_{pd}, with anisohydric species showing shallower slopes (Meinzer et al. 2016), and (ii)

$\Psi_{gs50\%}$ (MPa), that is, the Ψ_{leaf} value when stomatal conductance drops to 50% of the species maximum stomatal conductance, with increasingly negative values indicating more anisohydric behaviour (Klein 2014). Finally, pressure-volume curves were generated for five individuals per species during the dry season (Jun-Aug 2017), using the bench drying technique (Tyree and Hammel 1972), to obtain the leaf water potential at the turgor loss point (Ψ_{tlp}, MPa).

3.1.3.4 Data analysis

One-sample t-tests with a false discovery rate correction (FDR) were used to determine whether the FWU indices were significantly different from zero, and the Kruskal-Wallis H-tests were used to assess interspecific differences in FWU. To determine which CSR strategies and leaf traits were associated with FWU, we generated a Spearman rank correlation matrix with FDR-corrected p-values. As CSR strategies represent a triple trade-off, the CSR percentages are complementary; increases in the relative proportion of one strategy may lead to reductions in the other strategies. Despite this, correlation analyses between CSR percentages and FWU were conducted on each strategy separately (Rosado and de Mattos 2017) to better visualise how changes in the relative proportion contributed by a given strategy were associated with FWU. Subsequently, linear regression analyses were conducted to determine the strength of the relationships, but only the traits that were significantly correlated with FWU were used for this analysis. The linear regression assumptions were checked, and where necessary, a ln-transformation was applied to improve linearity, normality, and homoscedasticity. Following recommendations of de Bello et al. (2015), we did not conduct phylogenetic corretions during our analysis. All analyses were performed using R environments (R Core Team 2014), with $P < 0.05$.

3.1.4 Results

3.1.4.1 FWU interspecific variability

Most of the species (95%) had significant values of FWU, although there was a large variation in the quantity of water absorbed (FWU_{flux}: H = 276, df = 75, $P< 0.001$; FWU_{lwc}:H = 313, df = 75, $P< 0.001$), which ranged from 7.18 mg H_2O cm^{-2} $hour^{-1}$ in *H. lutea* to 0.34 mg H_2O cm^{-2} $hour^{-1}$in *Mimosa itatiaiensis* Dusén. There were also interspecific differences in FWU_{lwr} (H = 221, df = 75, $P< 0.001$), for 22% of the species, there was net water loss, indicating that the amount of water absorbed was not enough to rehydrate leaves.

3.1.4.2 Association between FWU and CSR strategies

The community was composed primarily of S species (72%), while 22% of the species were classified as C, and only 8% as R (Fig. 1). FWU was negatively associated with S% (FWU_{flux}: $R^2_{adj} = 0.18$, $P < 0.01$; Fig. 2a), positively associated with R% (FWU_{flux}: $R^2_{adj} = 0.12$, $P < 0.01$; FWU_{lwc}: $R^2_{adj} = 0.26$, $P < 0.01$; Fig. 2b,d), but was not correlated with C%. Increases in S% were associated with smaller LA and SLA, but higher LDMC; increases in C% were associated with greater LA, Lth, and SUC, but lower LDMC; and increases in R% led to smaller Lth, lower LDMC and SUC, but greater SLA. R% was positively correlated with Ψ_{tlp}, $\Psi_{gs50\%}$, Fsp, and stomatal conductance (g_{smean} and g_{smd}; Fig. 3).

3.1.4.3 Relationships between FWU and leaf traits

Mean values for leaf traits varied across species. The greatest variation was found for LA (mm²), which ranged from 7.12 (*C. capitata*) to 10, 795.16 (*L. tweediei*), and the smallest was found for Fsp (%), which ranged from 0.01 (*C. pinifolia*) to 0.07 (*M. glaziovi*). Appendix S2 provides the AIC, R², and parameter estimates for the model selected to obtain $\Psi_{gs50\%}$.

The two FWU indices were strongly associated with each other (Fig. 3). This association defined four distinct FWU behaviours ($R^2_{adj} = 0.37$; $P < 0.01$). The upper right quadrant (Fig. 4a) (i) was composed of a few highly efficient FWU species (*H. lutea*, *G.*

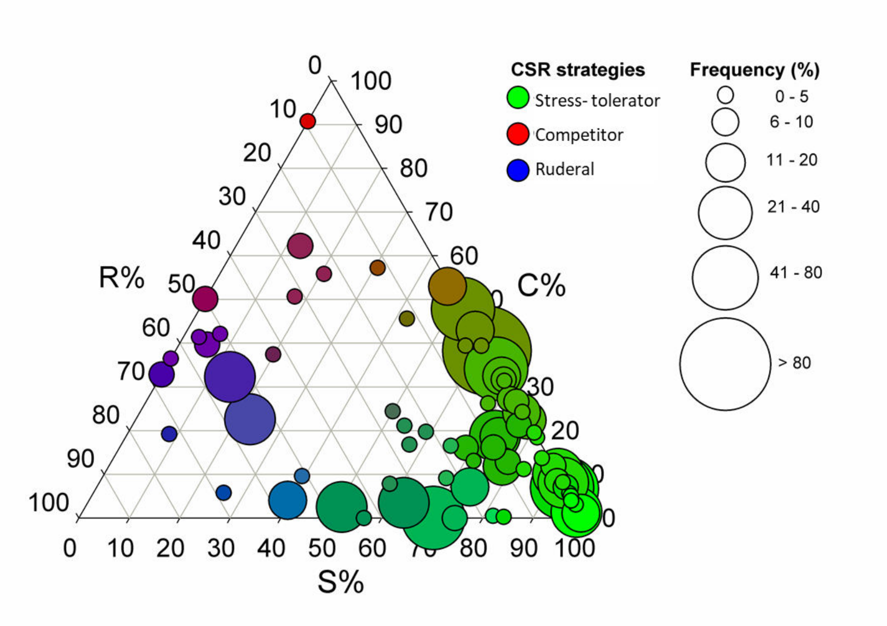
purpurea, and *Cerastium dicrotrichum*), which showed both higher FWU_{lwc} and higher FWU_{flux}. The lower left quadrant (ii) contained the majority of the evaluated species (n = 62), with lower FWU_{lwc} and lower FWU_{flux}. The other two quadrants represented combinations of low FWU_{flux} and high FWU_{lwc}(iii), and vice-versa (iv).

FWU_{lwc} was positively correlated with SLA ($R^2_{adj} = 0.37$; $P < 0.01$; Fig. 4b), and negatively correlated with Lth ($R^2_{adj} = 0.27$; $P < 0.01$; Fig. 4c), LA ($R^2_{adj} = 0.06$; $P = 0.01$; Fig. 4e), and SUC ($R^2_{adj} = 0.27$; $P < 0.01$; Fig. 4d). FWU_{flux} was positively associated with SLA ($R^2_{adj} = 0.16$; $P < 0.01$; Fig. 4h) but was negatively associated with LDMC ($R^2_{adj} = 0.23$; $P < 0.01$; Fig. 4i). Both FWU indices were positively associated with g_s (FWU_{lwc} x g_{smean}: $R^2_{adj} = 0.27$; $P = 0.04$; FWU_{lwc} x g_{smd}: $R^2_{adj} = 0.47$; $P < 0.01$; FWU_{flux} x g_{smean}: $R^2_{adj} = 0.70$; $P < 0.01$; FWU_{flux} x g_{smd}: $R^2_{adj} = 0.57$; $P < 0.01$; Fig. 4f-g,j-k).

3.1.5 Discussion

We found large interspecific variations in FWU that could be predicted from a combination of morpho-physiological leaf traits and ecological strategies. Insight into these patterns is important for understanding the ecological meaning of FWU, and may improve predictions of species and community stability under reductions in the frequency and duration of leaf-wetting events.

Figure 1 - CSR ecological strategies of 76 plant species from the *Campos de Altitude* - tropical mountain grassland (Itatiaia, RJ, Brazil).

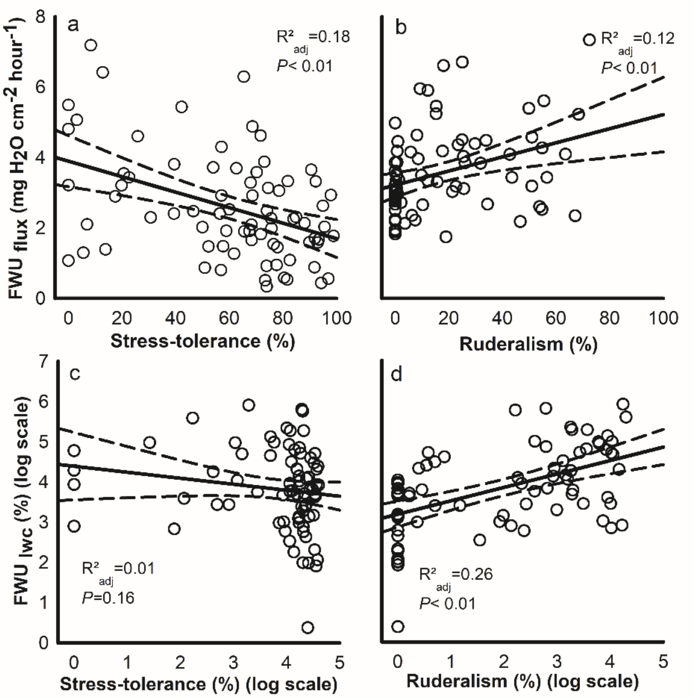


Subtitle: ecological strategies (competitiveness, C%; stress-tolerance, S%; ruderalism, R%). Circle sizes correspond to species frequency, and the colours were obtained by converting CSR coordinates into red, green, and blue, respectively.
Source: The author, 2019.

Although most of the species were able to absorb water through their leaves, thus confirming our first hypothesis (H1), this process did not always sufficiently compensate for water loss during the drying period. This finding provides further evidence that even in environments that are frequently subjected to leaf-wetting events, FWU may not be a common strategy used to cope with drought across co-occurring species (e.g. Limm et al. 2009, Goldsmith et al. 2012).

A negative relationship was found between stress-tolerance and FWU (Fig. 2a,c). In other words, leaf traits known to confer higher drought tolerance were associated with lower FWU, refuting hypotheses H2 and H3. Thus, the majority of species in the studied community may not have been directly dependent on FWU to withstand drought, and only a few species (those with lower S %) would have been able to efficiently absorb atmospheric water during drought.

Figure 2 - Results for linear regression between foliar water uptake (FWU) and CSR ecological strategies of 76 plant speciesfrom a *Campos de Altitude* - tropical mountain grassland (Itatiaia, RJ, Brazil).

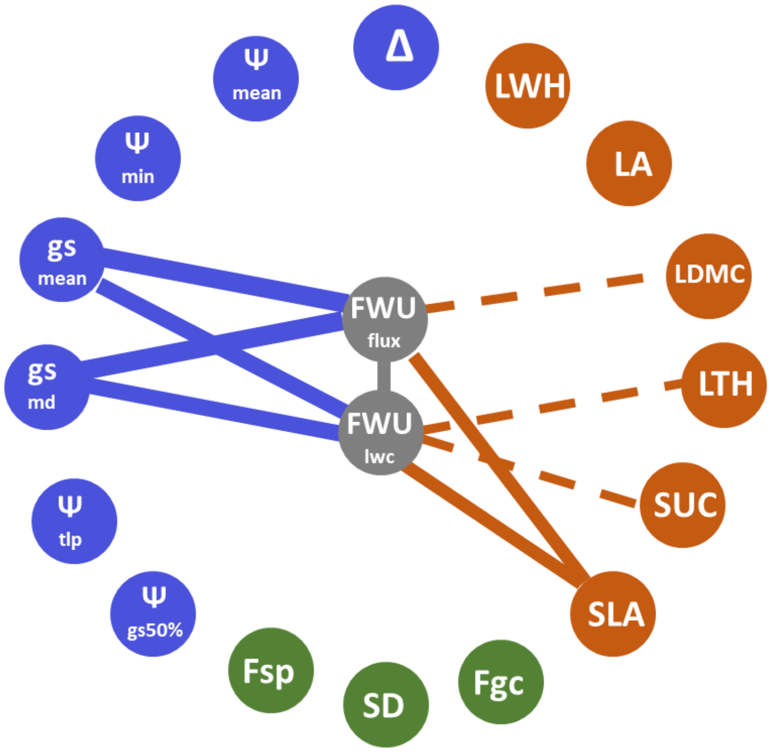


Subtitle: foliar water uptake (FWU_{flux} mg H_2O cm^{-2} $hour^{-1}$ and FWU_{lwc} %); CSR ecological strategies (stress-tolerance, S%; ruderalism, R%).
Source: The author, 2019.

In dry environments, a combination of smaller SLA and higher LDMC, leading to higher S %, may be accounted for by smaller and more tightly packed cells as well as by greater deposition of cell wall material throughout tissues (van Arendonk and Poorter 1997, Poorter et al. 2009). This may therefore result in tougher leaves (Ackerly et al. 2002), which prevent water loss during drought, but simultaneously minimise FWU in stress-tolerator species (Goldsmith et al. 2012, Gotsch et al. 2015). On the other hand, the tender leaves (large SLA, low LDMC) typical of lower S % species may be linked to higher leaf permeability, and thus promote FWU.

The apparent discrepancies between our results and those reported by Gotsch et al. (2015) may be associated somewhat with the different life-forms evaluated in each study (epiphytes/hemiepiphytes versus grasses/forbs/shrubs), and primarily with the distinct approaches used to assess species tolerance to drought. Gotsch et al. (2015) used Ψ_{tlp} as a proxy for drought resistance and considered that species with more negative values would be more tolerant to drought (Blackman et al. 2010, Bartlett et al. 2012). However, a greater ability to cope with droughtmay occur via avoidance (Gotsch et al. 2015), where species with less negative Ψ_{tlp} values may be able to close their stomata more rapidly, preventing turgor loss and maintaining higher hydration during water shortages (Bartlett et al. 2012). In our study, succulent species were less able to perform FWU (Fig. 4d), likely because greater leaf water storage may have prevented the formation of a driving gradient for water entry. Therefore, species with higher S % may be either tolerant or avoiders. This is one of the criticisms of the CSR scheme, which combines different strategies into one (Wilson and Lee 2000, Rosado and de Mattos 2017). Nevertheless, our finding, that the morphological traits that were linked to greater stress-tolerance (i.e. small SLA, high LDMC, and large Lth) and greater leaf water storage (i.e. high SUC and large Lth) exhibited less FWU, is in line with Gotsch et al. (2015), who also found that tougher and thicker leaves with a thicker leaf hydrenchymal layer showed limited FWU.

Figure 3 - Network of correlations between foliar water uptakeand leaf traits.

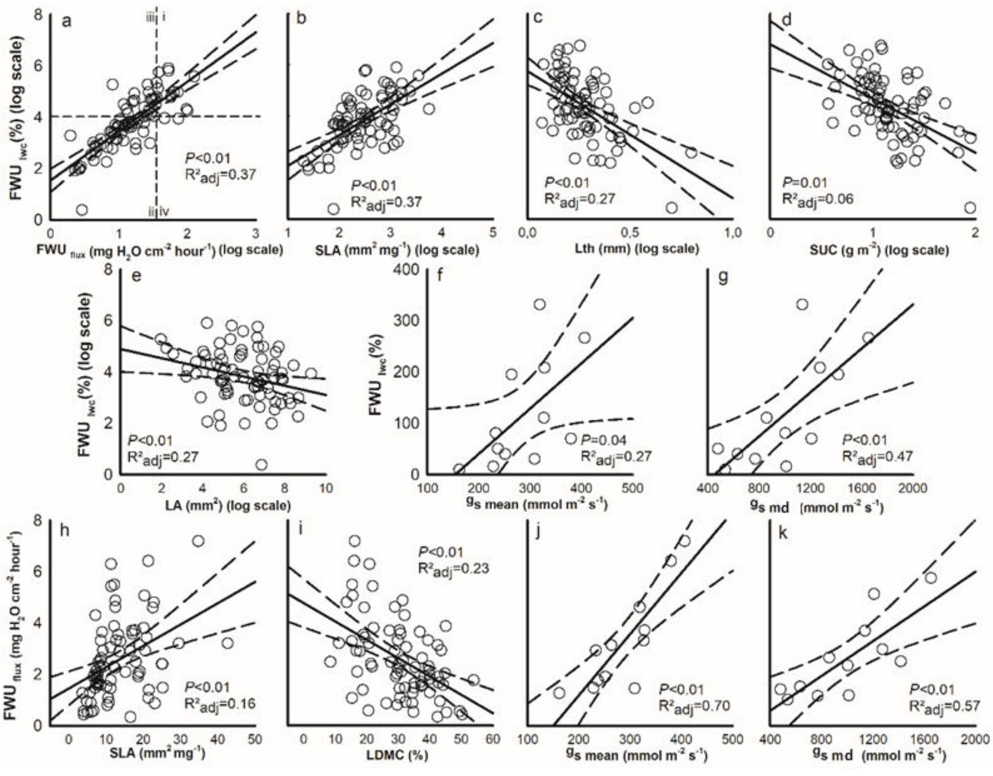


Subtitle:foliar water uptake (grey: FWU_{flux};FWU_{lwc}), and morphological (orange: LWH, LA, LDMC, LTH, SUC, SLA), anatomical (gree:Fgc, SD, Fsp), and physiological leaf traits (blue: $\Psi_{gs50\%}$, Ψ_{tlp}, $g_{s\ md}$,$g_{s\ mean}$, Ψ_{min}, Ψ_{mean}, Δslope), See Table 1 for abbreviations. Dashed and solid lines indicate negative and positive correlations, respectively. Correlation strength is represented by line thickness. Correlations between leaf traits are omitted.

Source: The author, 2019.

Beyond the importance of morphological traits, the positive relationship between FWU and stomatal conductance (Fig. 4f-g, j-k) suggested that stomata might play a role in FWU. Interestingly, FWU was not correlated with anatomical traits of stomata (SD, Fgc, and Fsp; Appendix S2B), indicating that it was not the number or size of the stomata *per se*, but the degree of pore aperture that was associated with a species FWU ability.

Figure 4 - Results of linear regression between foliar water uptake (FWU) and leaf traits of 76 plant species from the *Campos de Altitude* - tropical mountain grassland (Itatiaia, RJ, Brazil).



Subtitle: foliar water uptake (FWU_{flux} and FWU_{lwc}) and leaf traits: specific leaf area, SLA; leaf dry matter content, LDMC; leaf area, LA; leaf thickness, Lth; leaf succulence, SUC; mean midday stomatal conductance, g_{smean}; and maximum midday stomatal conductance, g_{smd}.

Source: The author, 2019.

Based on the above finding, we can make hypotheses about how additional mechanisms can be accounted for when evaluating FWU. If we consider FWU as a passive movement that is governed by differences in water potential between the inside and the surface of the leaf (Rundel 1982), species that sustain higher g_s would achieve lower Ψ_{leaf}, thereby creating a greater water potential gradient to promote FWU. Moreover, in the absence of specialised structures such as trichomes and hydathodes (Martin and von Willert 2000), it has been shown that water penetration can occur via cuticular (e.g. Gouvra and Grammatikopoulos 2003, Eller et al. 2013) and stomatal pathways (Burkhardt 2010). Therefore, a higher degree of stomata aperture could promote higher FWU, not only by creating a driving gradient during drying periods, but also by allowing water penetration during leaf-wetting events. To investigate this later hypothesis, however, it would be necessary to measure g_s and Ψ_{leaf} during FWU. Our measurements were taken seasonally under field conditions. Furthermore, one must consider that water exchange during FWU occurs in the liquid rather than the gaseous phase. Even though it was recently proposed that FWU could also occur in the gaseous phase by 'reverse transpiration' (Vesala et al. 2017).

Our results did not support the association between anisohydric behaviour and FWU that was previously proposed by Eller et al. (2016). Evaluating three tree species from a tropical montane cloud forest, Eller et al. (2016) found that the two anisohydric species had greater FWU than the isohydric species. They concluded that the maintenance of g_s at lower Ψ_{leaf} in the former species may favour FWU by creating a driving water potential gradient, while keeping the stomatal pathway open for water intake. Isohydric species, on the other hand, would be less dependent on leaf-wetting events, and could maintain leaf turgor during drought via tighter stomatal regulation (Eller et al. 2016). Such relationships, however, were not observed in our study, since no correlation was found between FWU and iso-/anisohydric behaviour. This reinforces the idea that there are issues associated with using iso-/anisohydric concepts (Hochberg et al. 2018) under contexts where variations in leaf water potential are directly dependent not only on stomatal conductance, but also on hydraulic conductance (Martínez-Vilalta and Garcia-Forner 2017). Furthermore, R% was positively correlated with $\Psi_{gs50\%}$ (Appendix S2B), that is, species with higher R% were prone to closing their stomata at less negative leaf water potential values. Thus, species with a higher proportion of R% (which exhibited higher FWU) showed less negative Ψ_{mean} and Ψ_{min} values across the seasons. Moreover, despite having tighter stomatal control, these species tended to have higher g_{smean} and g_{smd}, whereas species with higher S% showed the opposite pattern (Appendix S2B). Once more, these results indicated that FWU may be favoured by higher stomatal conductance (Berry et al. 2014), but not necessarily by lower leaf water potentials.

Based on the premise that FWU is a passive movement (Rundel 1982), it has been hypothesised that increases in water stress could maximise FWU by decreasing Ψ_{leaf}, thus creating a greater water potential gradient between the inside and the outside of the leaf (Limm et al. 2009). Indeed, a negative association between FWU and Ψ_{leaf} has been found in some studies (Breshears et al. 2008, Eller et al. 2016), but not in others (Burgess and Dawson 2004, Cassana et al. 2015), suggesting that a reduction in leaf surface water conductivity under stressed conditions could offset expected increased in the water flow gradient. Considering the stomatal and cuticular water entry pathways (Burkhardt 2010, Eller et al. 2013), reductions in leaf conductivity could be attributed to higher stomatal closure and/or cuticular hydrophobicity from dehydration (Cassana et al. 2015, Limm et al. 2009). In this study, we did not find a significant correlation between FWU and Ψ_{mean} and Ψ_{min} (Appendix S2B). However, it is important to highlight that Ψ_{mean} and Ψ_{min} were not measured during FWU, but were instead measured in plants under field conditions.

Regarding leaf hydrophobicity, it has been suggested that LWH could influence FWU by affecting the degree of water droplet spread onto the leaf surface, with less hydrophobic leaves being more prone to FWU (Oliveira et al. 2014). However, neither our results, nor those of previous studies (Goldsmith et al. 2016, Matos and Rosado 2016) have corroborated this association. The contact angle – a macroscopic parameter for static droplets that is currently used to determine LWH – may not sufficiently describe FWU. This is because, in the presence of hygroscopic particles, water-films can be formed even on very hydrophobic leaf surfaces (Eichert et al. 1998). In fact, Berry et al. (2014) found that under intense fog, the hydrophobic needles of two conifer species remained wet and exhibited FWU.

3.1.6 Conclusions

Co-occurring species differ in their ability for FWU, leading to differential responses to climate change. In this study, we showed that interspecific variability in FWU may be explained by leaf traits and ecological strategies. We found evidence that stress-tolerance is associated with morpho-physiological traits that decrease a species ability to perform FWU. Consequently, communities dominated by stress-tolerator species, like the *Campos de Altitude*, may be less likely to have their structure and functioning affected by ongoing increases in drought and reductions in the frequency of leaf-wetting events compared with communities dominated by species that employ other ecological strategies. However, even in such stress-tolerant communities, we may expect functional homogenisation Clavel et al. 2011), if reductions in leaf-wetting events result in the suppression of fog-dependent-ruderal species in favour of stress-tolerator species.

3.1.7 Acknowledgements

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3.1.8 References

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3.1.9 Supporting Information

Appendix S1 - Methods for morphological, anatomical and physiological leaf traits measurements

Appendix S2 - Results for models to obtain $\Psi_{gs50\%}$ for 12 species from Itatiaia, RJ, Brazil. Mean ± standard deviation (sd) of parameters, Akaike Information Criterion (AIC) and R^2 for the best fit model [linear: $g_s= a\Psi_{leaf}+b$; exponential: $g_s =c+ae -b\Psi_{leaf}$; logistic: $g_s = a/(1+(\Psi_{leaf}/c)b)$; or sigmoidal: $g_s= a/(1+e-((\Psi_{leaf}-c)/b))$]. $\Psi_{gs50\%}$ is the leaf water potential (Ψ_{leaf}) when the stomatal conductance (g_s) drops to 50% of its maximum.

Appendix S1 - Methods for morphological, anatomical and physiological leaf traits measurements

Frequency survey: we performed a frequency survey in the summer (peak standing biomass) using the quadrat method (Coulloudon et al. 1996), to support the choice of the species to be studied. Twelve 100-m transects were established within the study area, and for each transect 1 m²-quadrats were laid out at intervals of 3 m, totaling 300 m² of area sampled. All angiosperms rooted inside the plot, plus overhanging leaves or shoots were counted. Subsequently, species frequency was computed as the proportion of quadrats in which a species was observed. A subset of 76 species, comprising 84.8% of cumulative frequency, and including different life-forms (grasses, forbs and shrubs) and dominances (rare and dominant), were sampled to determine FWU, CSR strategies and a set of anatomical, morphological, and physiological leaf traits. During the frequency survey five species (*Fragaria vesca*, *Leptostelma tweediei*, *Lupinus gilbertianus*, *Plantago guilleminiana*, and *Symplocos itatiaiae*) did not occurred inside the plots, thus their frequency was zero. However, as they could be recurrently found in the areas around the plots, they were also included in the species trait measurements.

Morphological traits: we selected 10 individuals of each species, distant at least 10 m from each other, to measure morphological traits, following Pérez-Harguindeguy et al. (2013). Branchlets (for shrubs) or the whole individual (for herbs) were sampled in the early morning, temporarily stored in dark-plastic bags, recut into water and then rehydrated for about 2 h. From each individual, five mature leaves (excluding the petiole) were sampled to determine the water saturated fresh mass using a precision scale (0.01 g), and the leaf thickness (Lth, mm) using a digital calliper (0.01 mm). Following, leaves were scanned (300 dpi resolution) and then oven-dried at 50 °C for 72 h for determination of the dry mass. Leaf area (LA, mm²) was obtained from the digital image, using the software Image J version 1.48. Specific leaf area (SLA, mm^2 mg^{-1}) was calculated as leaf area/leaf dry mass; leaf dry matter content (LDMC, %) was obtained as leaf dry mass/leaf saturated mass; and leaf succulence (SUC, g m^{-2}) was measured as: (leaf saturated mass – leaf dry mass)/leaf area.

The mean water hydrophobicity for adaxial and abaxial leaf surfaces (LWH, degrees) was measured on three leaves per individual. Leaves were sampled, carefully dried with non-abrasive towel papers, and mounted horizontally on a Styrofoam platform. A 5 µL water droplet (miliQ) was placed on the leaf surfaces using a micropipette, then a photograph of the profile of the water droplet resting on the leaf surface was taken using a digital camera. The contact angle between the leaf surface and the line tangent to the droplet was measured using the software Image J version 1.48. The lower the contact angle, the less repellent is the leaf surface (lower LWH) (Matos and Rosado 2016, Rosado and Holder 2013). For seven species it was not possible to obtain the LWH, because their leaves were too small to fit a 5 µL droplet.

Anatomical traits: one leaf of five individuals per species was sampled, subjected to the diaphanization technique (Strittmater 1973) and mounted on glass slides. Digital photographs of both abaxial and adaxial leaf surfaces were taken up to a total of 1 mm² of area sampled per leaf surface, using a digital camera coupled in a light Microscope (Olympus Cx40, Spectra Services, Ontario, USA). The digital images were further analysed using the software Image Pro Plus version 4.5, to obtain: (1) stomatal density (SD, number mm^{-2}), i.e. the number of stomata per unit of leaf surface area; (2) average fraction of the leaf surface allocated to guard cell (Fgc, %), i.e. SD multiplied by the average area of the guard cell pair (de Boer et al. 2016), and (3) average fraction of the leaf surface allocated to stomatal pores (Fsp, %), i.e. SD multiplied by the average anatomical maximum stomatal pore area. It was not possible to obtain anatomical data for *Eryngium glaziovianum* because their leaves did not become translucent after diaphanization.

Physiological traits: midday stomatal conductance ($g_{s\ md}$, mmol $m^{-2}\ s^{-1}$); predawn leaf water potential (Ψ_{pd}, MPa); and midday leaf water potential (Ψ_{md}, MPa) were monthly measured, on three individuals per species, from June 2016 to June 2017, by using a steady-state leaf porometer (model SC1, Decagon Devices, Pullman, WA, USA) and a Scholander pressure chamber (model 1505D-EXP, PMS Instrument, Albany, OR, USA), respectively. From those data, we computed the mean midday stomatal conductance ($g_{s\ mean}$), mean midday leaf water potential (Ψ_{mean}), the maximum midday stomatal conductance ($g_{s\ md}$) and the minimum midday leaf water potential (Ψ_{min}) for each species.

Moreover, we used two different approaches to determine the aniso-isohydric behavior (Klein 2014, Martínez-Vilalta et al. 2014,Meinzer et al. 2016): (1) Δslope, the slope of a linear regression fitted to a plot of log(Ψ_{pd}- Ψ_{md}) vs. Ψ_{pd}, with anisohydric species showing lower slopes (Meinzer et al. 2016); and (2) $\Psi_{gs50\%,}$ the leaf water potential value when the stomatal conductance drops to 50% of the maximum stomatal conductance of the species, with a lower (more negative) value of $\Psi_{gs50\%}$ indicating a more anisohydric behaviour (Klein

2014). To compute the $\Psi_{gs50\%}$, linear, exponential, sigmoidal and logistic functions were fitted to the relationship between $g_{s\ md}$ vs. Ψ_{md}, using the optim function in R 2.9.2 (http://www.r-project. org). The maximum likelihood parameters were determined by the Simulated Annealing procedure for global optimization, followed by the Nelder–Mead simplex procedure for local optimization, standard errors for parameters were generated from the Hessian matrix, and the R^2 for observed values plotted against predicted values from the fitted function. The function with the lowest AIC value (corrected for low n) was chosen as the best fit function (Scoffoni et al. 2012).

Finally, pressure–volume curves were generated for five individuals per species during the drier season period (jun-ago 2017), by using the bench drying technique (Turner 1988). Plants were collected in field, stored in dark plastic bags and transported to the laboratory. Subsequently, stems or petioles were recut under water, and after 72 h of rehydration in darkness, they were weighed and promptly pressurized using a Scholander pressure chamber (model 1505D-EXP, PMS Instrument, Albany, OR, USA) for determination of the initial leaf water potential. Initial balancing pressures for sampling varied between 0.12 and 0.54 MPa. Leaves or twigs were allowed to dry on the bench and then the leaf water potential was measured again. This procedure was repeated until a sufficient number of data points for the pressure–volume analysis was generated. In general, this required at least three to five measurements in the linear portion of the pressure–volume isotherm, and at least four points before the turgor-loss point had been reached. Leaves were then placed in an oven at 70 °C for 48 h and reweighed to determine dry weight and calculate relative water content. A pressure–volume curve-fitting routine based on the template of Sack and Pasquet-Kok (2011), available in prometheuswiki (http://prometheuswiki.publish.csiro.au/tiki-index.php?page=Leaf+pressure-volume+curve+parameters), was used to obtain the leaf water osmotic potential at turgor loss point (Ψ_{tlp}, MPa) for each species. The Ψ_{tlp} is the negative water potential at which leaf cells lose turgor and the leaf wilts. At this point, water potential equals osmotic potential and subsequent declines in leaf water potential are because of increasing osmotic concentration (Bartlett et al. 2012).

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Appendix S2 - Results for models to obtain $\Psi_{gs50\%}$of 12 plant species from the *Campos de Altitude* - tropical mountain grassland (Itatiaia, RJ, Brazil).

Species	**Model**	**Parameters**			**AIC**	**R^2**	**$\Psi_{gs50\%}$**
		A	**B**	**c**			
Eryngium glaziovianum	Logistic	309.75 ± 20.68	4.48 ± 1.17	-2.09 ± 0.13	302.38	0.75	-2.09
Achyrocline satureioides	Logistic	578.79 ± 102.43	7.34 ± 3.67	-1.4 ± 0.09	287.45	0.73	-1.40
Baccharis uncinella	Linear	128.15 ± 16.30	376.19 ± 29.96		293.97	0.70	-1.47
Chionolaena capitata	Logistic	600.16 ± 89.67	1.76 ± 0.48	-1.16 ± 0.27	467.12	0.64	-1.16
Gamochaeta purpurea	Logistic	626.64 ± 89.73	1.64 ± 0.41	-1.93 ± 0.41	314.82	0.77	-1.93
Hypochaeris lutea	Logistic	598.08 ± 87.92	2.10 ± 0.75	-1.38 ± 0.26	470.25	0.58	-1.38
Leptostelma maximun	Linear	230.90 ± 30.15	586.65 ± 34.31		301.30	0.69	-1.27
Mikania glaziovii	Linear	228.41 ± 43.65	544.81 ± 54.45		307.77	0.51	-1.19
Machaerina ensifolia	Linear	105.77 ± 28.88	268.95 ± 38.06		283.37	0.35	-1.27
Pleroma hospital	Linear	145.26 ± 33.88	444.11 ± 40.14		255.93	0.44	-1.53
Chusquea pinifolia	Linear	68.05 ± 14.76	330.21 ± 25.88		281.13	0.45	-2.43
Cortaderia modesta	Linear	75.08 ± 12.45	374.36 ± 25.97		267.75	0.59	-2.49

Subtitle: mean ± standard deviation (sd) of parameters, Akaike Information Criterion (AIC) and R^2 for the best fit model [linear: g_s= aΨ_{leaf}+b; exponential: g_s =c+ae -bΨ_{leaf}; logistic: g_s = a/(1+(Ψ_{leaf}/c)b); or sigmoidal: g_s= a/(1+e-((Ψ_{leaf}-c)/b))]. $\Psi_{gs50\%}$ is the leaf water potential (Ψ_{leaf}) when the stomatal conductance (g_s) drops to 50% of its maximum.

Source: The author, 2019.

3.2 **Retain or repel? Droplet volume does matter when measuring leaf wetness traits**

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Running title**:** Drop-volume effect on leaf wetness traits

3.2.1 Abstract

Background and Aims Leaf wetness is an important characteristic linked to a plant strategy for water acquisition, use and redistribution. A trade-off between leaf water retention (LWR) and hydrophobicity (LWH)may be expected, since a higher LWH/lower LWR may enhance photosynthesis, while the opposite combination may increase the foliar wateruptake(FWU). However, the validation of the ecological meaning of both traits and the influence of droplet volume when measuring them have been largely neglected.

Methods To address these questions, LWR and LWH of 14 species were measured using droplets ranging from 5 to 50 µL. Furthermore, the ability of those species to perform FWU was evaluated through leaf submergence in water. The droplet-volume effect on absolute values and on species ranking for LWR and LWH was tested, as well as the influence of water droplet volume on the relationship between leaf wetness traits and FWU.

Key Results Variations in droplet volume significantly affected the absolute values and the species ranking for both LWR and LWH. The expected negative correlation between leaf wetness traits was not observed, and they were not validated as a proxy for FWU.

Conclusions The water droplet volume does matter when measuring leaf wetness traits. Therefore, it is necessary to standardize the methodological approach used to measure them. The use of a standard 5 µL droplet for LWH and a 50 µL droplet for LWR is proposed. It is cautioned that the validation of both traits is also needed before using them as proxies to describe responses and effects in functional approaches.

Key words: Contact angle, hysteresis, foliar water uptake, leaf hydrophobicity, leaf water repellency, leaf water retention, throughfall.

3.2.2 Introduction

Plant species differ greatly in their ability to retain or to repel water droplets on leaf surfaces (Neinhuis and Barthlott 1997, Aryal and Neuner 2010). After leaf wetness events caused by rain, fog, dew or mist, super-hydrophilic leaves may become covered by a water film or by many flattened droplets, while highly non-wettable surfaces may repel water by forming almost spherical-shaped droplets. In some species, the water droplets easily drain off of the leaves, but in others they remain strongly adhered to foliar surfaces even at steeper leaf inclination angles (Brewer et al. 1991, Aryal and Neuner 2010). These differences in leaf water hydrophobicity (LWH) and leaf water retention (LWR) may reflect distinct strategies related to plant water acquisition, use and redistribution (e.g. Holder 2007, Aryal and Neuner 2010).

As the presence of a water film on the leaf surface can significantly reduce the gas exchange by reducing CO_2 diffusion and occluding stomatal apertures, there should be a strong selective pressure to repel water droplets from the leaf surface, especially for plants inhabiting very wet areas (Smith and McClean 1989, Brewer et al. 1991, Holder 2012). In fact, this hypothesis has been corroborated by studies that found higher LWH and lower LWR values in species from open areas – where leaf wetness events are generally more frequent (Jordanand Smith 1994) – than in understory species (e.g. Brewer and Smith 1997, Pandey and Nagar 2003).

In arid and semi-arid environments, plants may exhibit highly repellent leaf surfaces due to the presence of high-density trichomes and hydrophobic epicuticular waxes (Holder 2012). Usually seen as a specialization to minimize water loss and overheating (Schreuder et al. 2001), these features can also promote low leaf wettability and then contribute to higher throughfall rates during the rare periods of precipitation (Holder 2012). Hence, in such habitats, highly repellent leaves might not only enhance gas exchange and photosynthetic efficiency, but also increase water availability to root systems (Holder 2012). Additionally, by avoiding the persistence of water films on leaves, plants can also reduce the incidence of pathogens (Reynolds et al. 1989), the colonization of epiphylls (Holder 2007), pollutant deposition (Neinhuis and Barthlott 1998, Klemm et al. 2002), ice formation (Aryal and

Neuner 2010) and tissue damages caused by focusing sunlight (Brewer et al. 1991). Therefore, repelling water droplets from leaves seems to be an advantage in either wet or dry environments since it may be related to distinct ecological processes (Smith and McClean 1989, Brewer et al. 1991, Holder 2007, Rosado et al. 2010). However, staying wet all over is not always detrimental. Under some circumstances, an ability to retain water droplets on leaves, instead of repelling them, can be beneficial to plants. The evaporation of water films reduces leaf temperature, eases heat stress and decreases transpiration rates (Katata et al. 2010). As a result, plants can absorb CO_2 at a low water cost and keep a positive carbon balance, even under soil water deficits (Simonin et al. 2009, Ben-Asher et al. 2010). Some plants are also able to absorb water directly through their leaves (Goldsmith et al. 2013). It has been shown that foliar water uptake (FWU) can contribute up to 42% of the total leaf water content (Eller et al. 2013) and can significantly improve plant water status, by decreasing stomatal conductance, recovering xylem cavitation, increasing shoot water potential and positively affecting plant survivorship and growth (Limm et al. 2009, Simonin et al. 2009, Eller et al. 2013). In areas where dew and fog events co-occur with dry-soil conditions, FWU may be an important mechanism for plant hydration (e.g. Limm et al. 2009, Goldsmith et al. 2013), and then a selective pressure for reducing LWH and increasing LWR should be expected (Simonin et al. 2009, Rosado and Holder 2013). Alternatively, lower LWH observed in plants exposed to artificial fog (Eller et al. 2013) or inhabiting moist forests (Neinhuis and Barthlott 1997) and fog-affected environments (Holder 2007) may be simply caused by the erosive effect of the water on leaf epicuticular waxes, and does not necessarily reflect an adaptive plant response.

Since leaf wetness events may have both negative and positive effects, a continuum is expected between the two opposite plant strategies, from the species able to perform FWU (lower LWH and higher LWR) to the species that avoid water films on the leaf surfaces by throughfall (higher LWH and lower LWR) (Konrad et al. 2012, Fernández et al. 2014). Although quite plausible, the relationships among leaf wetness traits and these ecophysiological processes have not yet been validated at the species or community levels. As proposed by Rosado et al. (2013), the validation of traits is needed to test whether they can truly be used as proxies to predict plant responses. Furthermore, the relationship between LWH and LWR is uncertain, since the expected negative correlation has been found in some studies (Brewer and Smith 1997, Brewer and Nuñez 2007), but not in others (Pandey and Nagar 2003, Holder 2012).

The discrepancy among studies may be related to methodological artefacts in the functional trait-based approach used to evaluate LWH and LWR. Usually, LWH has been assessed by calculating the contact angle between the leaf surface and the line tangent to a sessile water droplet through the point of contact (Aryal and Neuner 2010, Rosado and Holder 2013). As the contact angle increases, the amount of leaf area covered by the water droplet decreases. Thus, greater contact angles indicate a more spherical water droplet and a more water-repellant surface (Rosado and Holder 2013). In turn, LWR has been defined as the angle of tilt in which a water droplet begins to move or downslide as a leaf is incrementally tilted from 0 to 90°. High angular values indicate a greater tendency to retain droplets, while low values indicate leaf surfaces that readily shed droplets (Brewer 1996).

According to Brewer (1996), these measurements could be made using droplets of different sizes to simulate different leaf wetness sources, such as rain, fog, dew or garden sprinklers. Reviewing several papers that measured leaf wetness traits, Rosado and Holder (2013) found that water droplets from 1 to 10 µL (5 µL is the most often used) have been used to determineLWH, while for LWR the range is from 10 to 50 µL (50 µL is the most often used). In the handbook for the measurement of plant traits, Pérez-Harguindeguy et al. (2013) suggested droplets from 2 to 5 µL to measure LWH, but no standard value was proposed for LWR. Although Schreiber (1996) found that there were no significant differences for LWH among droplets from 1 to 10 µL, this study was performed on only one species, which reduces the possibility of expanding this result to create a general rule. To the best of our knowledge, there have not yet been any studies investigating whether water droplet size influences LWR.

Taking into account the importance of leaf wetness for ecological processes in different hierarchical levels (e.g. from leaf to ecosystem), our aims were as follows: (a) to test if the changes in droplet water volume significantly affect the values of LWH and LWR, as well as the relationship between these two traits; (b) to evaluate the consistency of species ranking based on these traits when using different water droplet volumes; and (c) to validate whether these traits may be used as proxies to predict species ability to perform FWU.

3.2.3 Materials and methods

3.2.3.1 Sites and species

We collected leaves of 14 species from two sites: Parque Nacional da Floresta da Tijuca and Parque Nacional do Itatiaia, both located in Rio de Janeiro state, Brazil (Table 1). Tijuca Forest (22°57'S, 43°18'W) is a remnant of the Atlantic rain forest located inside Riode Janeiro city, and has a tropical wet climate (Aw, Köppen classification) with a mean annual temperature of 21 °C and a mean annual precipitation of 2500mm (Brasília 2008). The tropical mountain grassland of Itatiaia (22°21'S, 44°40'W; about 2400 m asl) is covered by grassland vegetation and has a high land tropical climate (Cwb, Köppen classification) with a mean annual temperature of 18 °C and a mean annual precipitation of 2400mm (Segadas-Vianna and Dau 1965, Safford 1999). The selected species are common in their sites, differ in the presence/ absence of foliar trichomes and have leaves large enough to enable the allocation of droplets of different volumes.

3.2.3.2 Measurement of leaf wetness traits

Ten branches of each species were collected (May and June 2015), transported to the laboratory and stored in the refrigerator until the measurements. For each branch, five mature healthy leaves were sampled, dried with a non-abrasive absorbent filter paper and pinned onto a Styrofoam flat platform. A droplet of milli-Q water was placed onto the leaf surface using a micropipette (P100, Pipetman, Gilson SAS, Villiers-le-Bel, France). To measure LWH, a photograph of the water droplet resting on the horizontal leaf surface was taken with a digital camera (Exmor R CMOS, ½.3'', 20.4 Megapixel, Sony, Tokyo, Japan). From the digital image, the contact angle was determined using the free software Image J, version 1.48. To measure LWR, the platform was progressively tilted from 0 to 90°, and the angle of tilt in which the water droplet moved was determined using a protractor. A retention angle of 90° was assigned to the samples that, after the complete tilting of the platform, did not show droplet movement. To consider the range of droplet volumes observed in the literature (Rosado and Holder 2013), LWR and LWH were measured using water droplets of five different volumes: 5, 10, 15, 25 and 50 µL. Measurements of both adaxial and abaxial leaf surfaces on 50 leaves per species, ten for each droplet volume, were conducted.

Table 1 - Mean ± standar deviation values for leaf wetness and foliar water uptake for 14 species from the Atlantic Rain Forest (Parque Nacional Floresta da Tijuca – PNT) and the Tropical Mountain Grassland (Parque Nacional do Itatiaia – PNI), Rio de Janeiro, Brazil.

Family	**Species**	**Site**	**LWR (degrees)**	**LWH (degrees)**	**FWU (%)**	**Trich. AD**	**Trich. AB**
Fabaceae	*Inga vera*Willd.	PNT	61.0 ± 27.7	53.8 ± 14.9	28.4 ± 10.7	P	P
Melastomataceae	*Leandra dasytricha* (A.Gray) Cogn.	PNT	56.9 ± 31.8	42.5 ± 10.0	42.6 ± 4.2	P	P
Myrtaceae	*Myrciaspectabilis* DC.	PNT	44.4 ± 27.4	68.1 ± 16.4	22.7 ± 14.9	P	P
Piperaceae	*Piper sp*	PNT	32.6 ± 14.3	41.4 ± 9.4	10.6 ± 3.9	P	P
Rubiaceae	*Psychotria nuda* (Cham. &Schltdl.) Wawra	PNT	41.9 ± 17.9	49.2 ± 11.5	38.2 ± 18.3	A	A
Rubiaceae	*Psychotria sp*	PNT	49.1 ± 15.3	54.1 ± 11.3	29.0 ± 11.1	A	A
Rubiaceae	*Psychotria leiocarpa* Cham. & Schltdl.	PNT	38.7 ± 12.2	53.3 ± 9.6	56.5 ± 23.8	A	A
Asteraceae	*Baccharis stylosa* Gardner	PNI	18.8 ± 7.1	52.3 ± 10.4	37.3 ± 10.0	P	P
Asteraceae	*Baccharis itatiaiae* Wawra	PNI	10.3 ± 4.6	55.7 ± 7.4	37.6 ± 9.7	A	A
Asteraceae	*Senecio adamantinus* Baker	PNI	21.8 ± 12.5	77.2 ± 24.5	-	P	P
Asteraceae	*Graphistylis itatiaiae* (Dusén) B. Nord.	PNI	15.8 ± 14.9	60.4 ± 7.4	60.1 ± 28.0	A	P
Asteraceae	*Achyrocline satureioides* (Lam.) DC.	PNI	8.0 ± 3.5	117.5 ± 9.4	30.7 ± 12.6	P	P
Cyperaceae	*Machaerina ensifolia* (Boeckeler) T. Koyama	PNI	15.3 ± 6.0	65.2 ± 7.1	9.6 ± 2.8	A	A
Ericaceae	*Gaultheria serrata* (Vell.) Sleumer ex Kin.-Gouv.	PNI	23.2 ± 8.6	51.6 ± 6.9	13.9 ± 9.1	P	P

Subtitle: leaf water retention (LWR) measured using a 50 µL water droplet; leaf water hydrophobicity (LWH) measured using a 5 µL water droplet;foliar water uptake(FWU) measured as the percentage of increase in leaf water content after leaf submergence in distilled water; and presence (P) or absence (A) of trichomes on adaxial (AD) and abaxial (AB) leaf surfaces.

Source: The author, 2019.

3.2.3.3 Measurement of foliar water uptake

The ability of a species to perform FWU was determined based on the protocol proposed by Limm et al. (2009). For each species, five branches were collected, placed between damp sheets of paper, sealed in zip-lock bags and maintained at 5 °C in the dark for 72 h to ensure a standard degree of turgor for all samples. After rehydration, one mature healthy leaf per branch was chosen and allowed to dry on the bench for 3 h in a 20 °C room. The initial mass (m_1) was determined and then the petiole was sealed with vaseline to prevent water entry. The whole leaf lamina was submerged in distilled water in darkness. The complete leaf submergence was used to standardize water availability across the morphologically diverse foliar types and represented the maximum quantity of water that a plant could absorb through the leaves. After 3 h, the leaf was removed from the water, dried with paper towels and the mass after this first submergence was recorded (m_2). To account for any potential error associated with residual water on the leaf surface, the leaf was allowed to dry on the bench for 5min and then the mass was recorded again (m_3). The same leaf was re-submerged in water for 1 s, dried with paper towels and immediately reweighed (m_4). This brief re-wetting did not allow sufficient time for water absorption, so any increase in mass associated with this second submergence represented the residual water on the leaf surface. Finally, all leaves were dried at 50 °C for 96 h to determine the dry mass (m_{dry}). The ability of a species to perform FWU was calculated as the increase in leaf water content after submergence, using: $\text{FWU}\ (\%) = \{[m_2 - (m_4 - m_3) - m_{dry}]/(m_1 - m_{dry}) - 1\} \text{ x } 100$. For one species, it was not possible to perform the FWU experiment, due to a lack of sufficient samples.

3.2.3.4 Statistical analysis

Nested analysis of variance (ANOVA) followed by pairwise t-tests were used to assess whether there were significant differences in LWR and LWH values among sites, species, leaf faces and droplet volumes. Species were nested within sites, leaf faces within species, and droplet volumes within leaves (Holder 2007, Rosado et al. 2010). Spearman rank correlation was used to verify the consistency in the species ranking across the different droplet volumes used to measure LWR and LWH. Small and non-significant coefficients indicate more changes in species ranking among the droplet volumes (Garnier et al. 2001, Rosado and de Mattos 2007). Analysis of covariance (ANCOVA) was used to verify whether the relationship between LWR and LWH was affected by the water droplet volume, and Spearman correlation was used to test the relationship between leaf wetness traits and FWU. A one-sample t-test was used to determine if the increase in percentage FWU after the first submergence was significantly higher than 0%. All statistical analyses were performed using the R environment (R Development Core Team 2014) at a significance level of α =0.05.

3.2.4 Results

Leaf water retention and hydrophobicity differed significantly among sites, species, leaf faces and droplet volumes (Table 2; Supplementary Data Fig. S1, Tables S1 and S2). Leaf wetness trait values varied according to the droplet water volume used (Fig. 1). For LWR, there were no significant differences between droplets of 5 and 10 µL (Fig. 1A). These small droplets rarely dripped from the leaves, thus all species showed high retention values when these volumes were used (mean LWR for all species together: 5 µL droplet = 88.7°; 10 µL droplet = 86.5°). With an increase in the droplet volume, LWR decreased, reaching the minimum value for all species when measured with 50 µL droplets. LWH values were less variable among droplet volumes (Fig. 1B), and significant differences were found only for 15 µL droplets. A drop-volume effect was also observed for species ranking (Fig. 2). A higher number of low and non-significant Spearman rank coefficients were found for LWR than for LWH (Table 3). ANCOVA results also showed that LWR values were significantly affected by the droplet volume (ANCOVA; $F = 35.7$, d.f. = 4, $P < 0.001$). The relationship between LWR and LWH was not significant for any of the droplet volumes tested (ANCOVA; $F = 3.54$, d.f. = 1, $P = 0.06$, Fig. 3). All sampled species were able to perform FWU (Table 1). Nevertheless, the percentage increase in FWU varied among species, ranging from 9.6% in *Machaerina ensifolia* to 60.1% in *Graphistylis itatiaiae*. No significant relationships were found between FWU and leaf wetness traits (Fig. 4) (Spearman rank correlations: LWR, q = –0.02, P =0.94; LWH, q = –0.08, P = 0.77).

Table 2 - Summary of results of the nested ANOVA for leaf water retention and leaf water hydrophobicity.

Summary of Nested ANOVA	**Df**	**SS**	**MS**	***F***
Retention				
Sites	1	97028	97028	606.53***
Sites: species	12	39477	3290	20.56***
Sites: species: leaf face	14	27018	1930	12.06***
Sites: species: leaf face: droplet volume	112	770873	6883	43.02***
Hydrophobicity				
Sites	1	92867	92867	932.13***
Sites: species	12	355363	29614	297.24***
Sites: species: leaf face	14	63562	4540	45.57***
Sites: species: leaf face: droplet volume	112	48374	432	4.33***

Subtitle: nominal variables: sites (Atlantic Rain Forest and Tropical Mountain Grassland), species (seven common species from each site), leaf faces (adaxial and abaxial), and droplet volumes (5, 10, 15, 25, and 50 µL). Species were collected from two sites: Parque Nacional da Floresta da Tijuca (Atlantic Rain Forest) and Parque Nacional do Itatiaia (Tropical Mountain Grassland), Rio de Janeiro, Brazil. $^{***}P < 0.001$.

Source: The author, 2019.

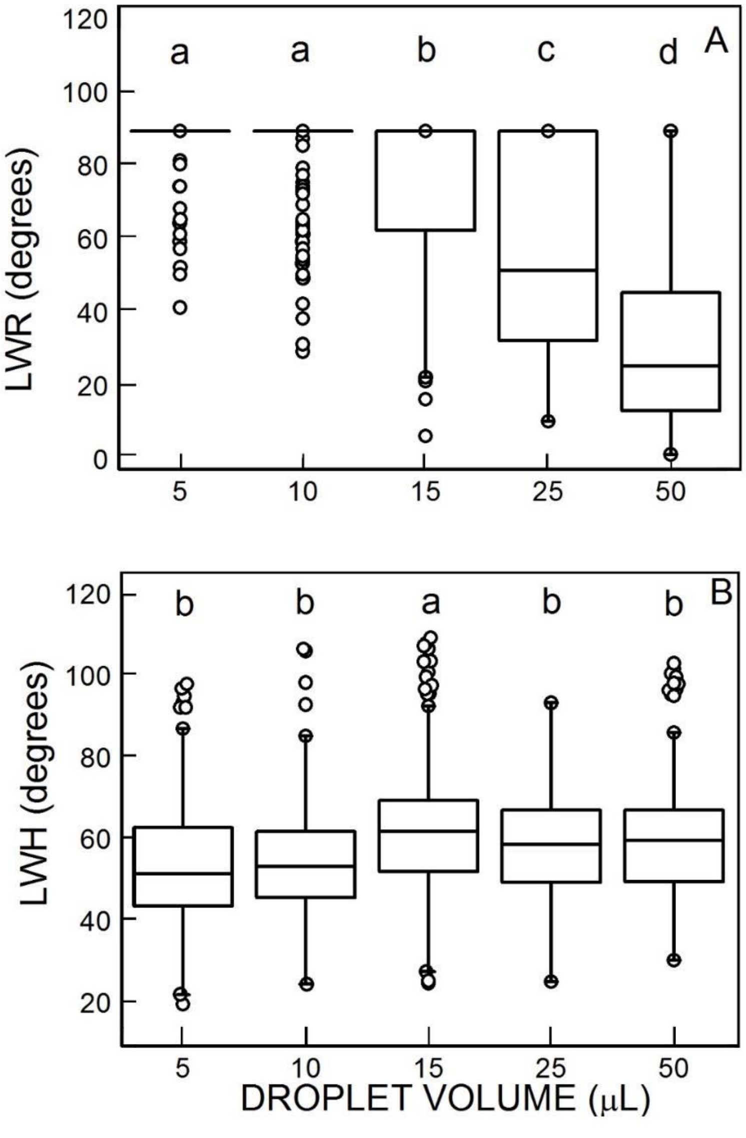
Table 3 - Spearman rank correlation coefficients comparing the ranking of 14 plant species (from Parque Nacional da Floresta da Tijuca - Atlantic Rain Forest and Parque Nacional do Itatiaia - Tropical Mountain Grassland, both located at the Rio de Janeiro, Brazil) in relation to leaf water retention and hydrophobicity measured with five different droplet volumes (5, 10, 15, 25, and 50 µL).

Spearman rank correlation coefficients	**Droplet volume (µL)**	50	25	15	10
Retention	5	0.20	0.28	0.48	0.40
	10	0.24	0.09	**0.61**	
	15	**0.69**	0.52		
	25	**0.63**			
Hydrophobicity	5	0.48	0.50	**0.54**	**0.75**
	10	0.51	**0.55**	**0.61**	
	15	**0.93**	**0.91**		

25	**0.91**

Subtitle: Bold values indicate significant correlations (*P*< 0.05)

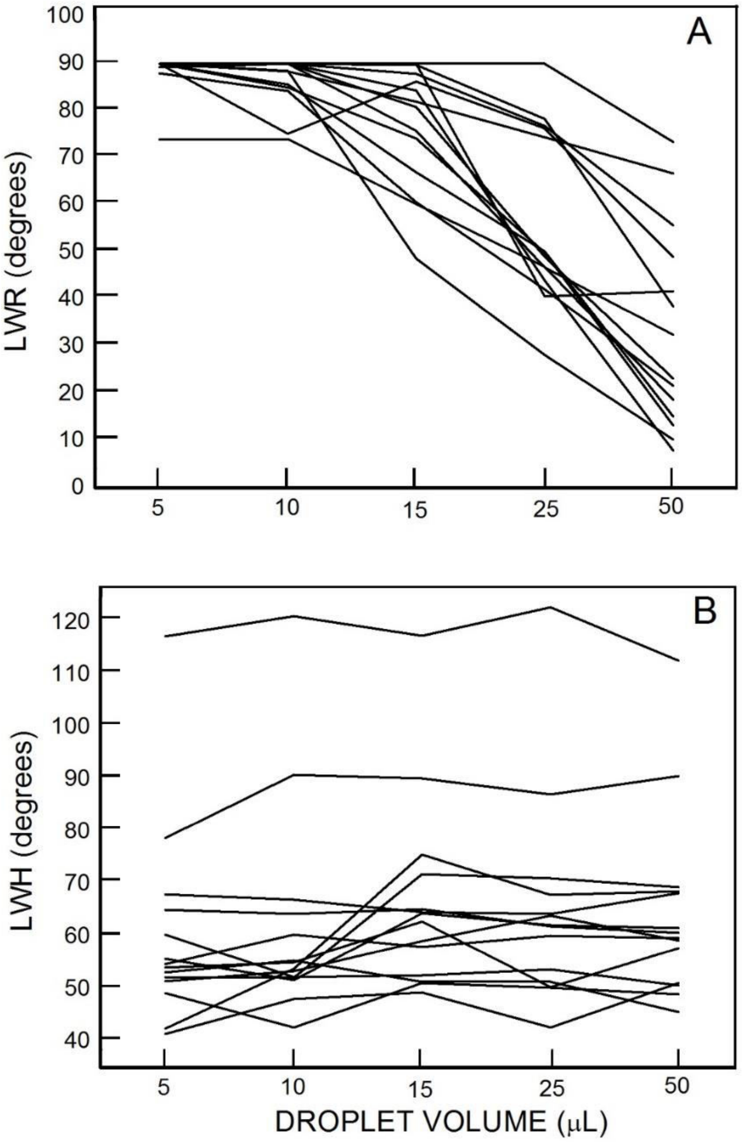
Figure 1 - Variation in leaf wetness across five droplet water volumes for 14 plant species.



Subtitle:mean values ± SD for leaf water retention LWR (**A**) and hydrophobicity LWH (**B**) for five droplet volumes (5, 10, 15, 25, and 50 μL). Letter codes indicate homogeneous groups among species (pairwise t-test, *P* < 0.05, adjusted with Bonferroni correction method). Species were collected from two sites: Parque Nacional da Floresta da Tijuca (Atlantic Rain Forest) and Parque Nacional do Itatiaia (Tropical Mountain Grassland), Rio de Janeiro, Brazil.

Source: The author, 2019.

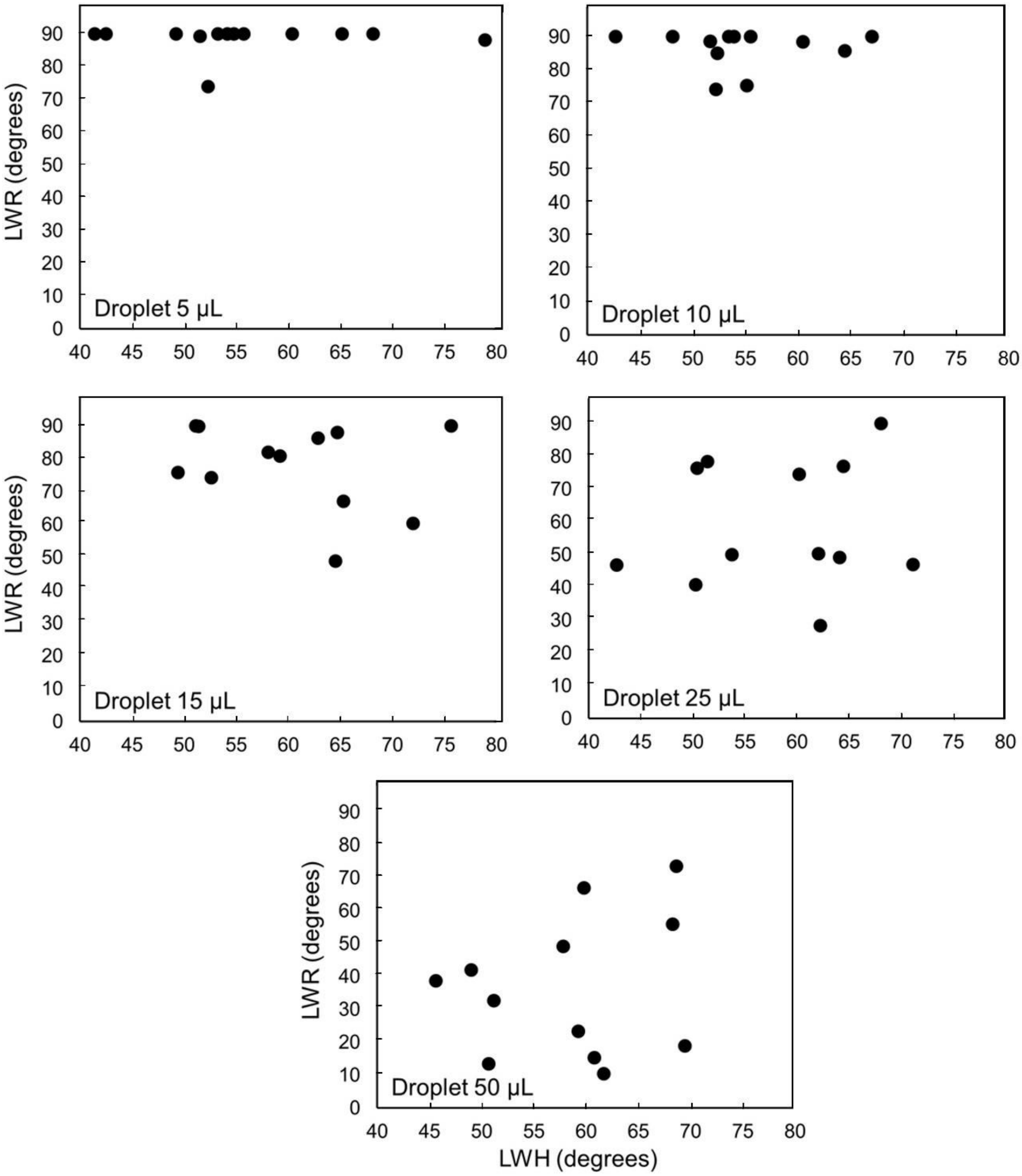
Figure 2 - Leaf wetness for five water volumes and 14 plant species.



Subtitle:leaf water retention LWR (**A**) and hydrophobicity LWH (**B**) for each water droplet volume (5, 10, 15, 25, and 50 μL) for 14 species analyzed, seven from the Atlantic Rain Forest (Parque Nacional da Floresta da Tijuca) and seven from the Tropical Mountain Grassland (Parque Nacional do Itatiaia), Rio de Janeiro, Brazil. Each line represents one species, and the crossing of lines indicates changes in species ranking.

Source: The author, 2019.

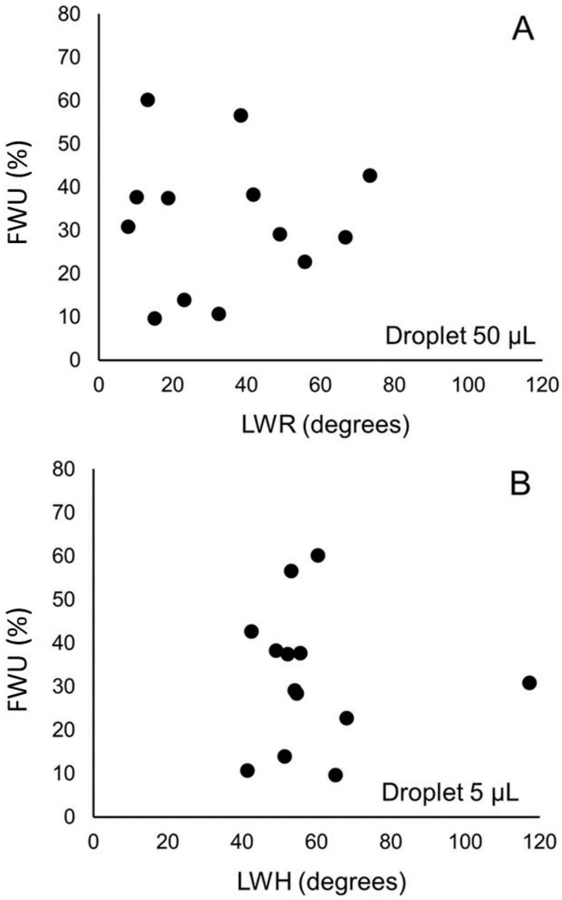
Figure 3 - Relationships between leaf wetness and droplets water volume.



Subtitle: relationship between leaf water retention (LWR) and hydrophobicity (LWH) for each droplet volume (5, 10, 15, 25, and 50 µL) for 14 species from the Atlantic Rain Forest (Parque Nacional da Floresta da Tijuca) and the Tropical Mountain Grassland (Parque Nacional do Itatiaia), Rio de Janeiro, Brazil.

Source: The author, 2019.

Figure 4 - Relationship between leaf wetness and foliar water uptake for 14 plant species from the Atlantic Rain Forest (Parque Nacional da Floresta da Tijuca) and the Tropical Mountain Grassland (Parque Nacional do Itatiaia), Rio de Janeiro, Brazil.



Subtitle: leaf water retention LWR (**A**) leaf water hydrophobicity LWH (**B**), and foliar water uptake (FWU) measured as the percentage of increase in leaf water content after leaf submergence in distilled water.
Source: The author, 2019.

3.2.5 Discussion

Changes in droplet volume significantly affected the measurement of leaf wetness traits, but LWR was more affected than LWH. Although previously unexplored for leaf surfaces, the drop-volume effect on retention and hydrophobicity properties has been a subject of many debates in material and chemistry sciences (e.g. Drelich et al. 1993, McHale et al. 2004, Vafaei and Podowski 2005, Das and Das 2010, Cansoy 2014). Hence, before we can determine the functional meaning of leaf wetness traits, we must first attempt to understand the physical processes behind the drop-volume effect.

3.2.5.1 The drop-volume effect on leaf wetness traits

The hydrophobicity of any material (including leaves) is a property of the liquid–solid system and, at first, only depends on the balance between adhesive forces that favor spreading (acting between the liquid and the solid surfaces) and the counteracting cohesive forces (among liquid molecules) (Vafaei and Podowski 2005, Lamour et al. 2010). This material-dependence principle, however, is valid only until a critical droplet volume is reached (Vafaei and Podowski 2005). Thus, the contact angles will only be affected by the droplet volumes after this threshold has been exceeded. From this point forward, gravity starts deforming the droplet shape, and progressive increases in drop volume tend to reduce the contact angles (Drelich et al. 1993). Thus, for large drops, the contact angle is governed by the liquid volume rather than by the solid surface traits (Vafaei and Podowski 2005, Das and Das 2010).

For pure water, the critical droplet volume is about 10 μL. Therefore, droplets larger than 10 μL should not be used to measure contact angles (Cansoy 2014). In fact, in our study, the drop-volume effect on LWH was detected after this threshold, i.e. significant differences in LWH were found for 15 μL droplets, but not for 5 or 10 μL droplets. However, the reason why only the 15 μL droplets, and not the 25 or 50 μL droplets, differed from the other volumes is not clear. This threshold may also explain why Schreiber (1996) did not find a significant drop-volume effect on LWH values, since, in his study, droplets only ranged from 1 to 10 μL. As most of the studies about leaf wetness have used droplets of 5 μL to measure LWH (Rosado and Holder 2013), we propose that this value should be adopted as the standard to determine the contact angle on leaf surfaces, providing a safety margin to prevent a drop-volume effect on LWH measurements.

The detachment or sliding down of a droplet on an inclined surface also depends on the occurrence of a critical droplet volume because droplets only begin to move when the gravity forces are greater than the surface forces (Konrad et al. 2012). For most of our species, the critical volume was surpassed with 15 µL droplets, since the 5 and 10 µL droplets were rarely shed. Droplets of 50 µl, which simulate very large raindrops, have been used to measure LWR in the majority of the studies on this issue (Rosado and Holder 2013). On the one hand, the use of 50 µl as a standard ensures that the critical volume will be exceeded for most species, but on the other hand, it brings, at least, two methodological problems. First, as mentioned above, for large drops, gravity might be more important than surface properties for determining the degree of droplet retention. Secondly, this trait becomes immeasurable in small-leaf species, on which droplets of 50 µL simply do not fit. A small leaf area is a common trait in plants subjected to abiotic stresses (cold, drought, heat and high radiation) (Cornelissen et al. 2003); thus, the impossibility of measuring LWR in these species makes it infeasible to compare leaf wettability along environmental gradients. These comparative studies are essential to gain an understanding of the degree of convergence among leaf wetness traits in similar habitats around the world, as well as for investigating their actual impact on ecohydrological processes (Brewer and Nuñez 2007, Rosado and Holder 2013).

As shown in this study, not only the absolute trait values, but also the species ranking varied depending on the droplet volume used to measure LWR and LWH. Therefore, studies that have used different droplet sizes are not comparable, which reinforces the need for a standard method in leaf wetness measurements. It is remarkable that classifications based on LWH were more repeatable among different droplet volumes than those based on LWR. The higher consistency in species ranking for hydrophobicity and the possibility of measuring this trait in smaller-leaf species (on which 5 µL droplets would fit) recommend the use of this functional trait to compare the ability of different species to retain or repel water, rather than the use of leaf water retention (LWR).

3.2.5.2 Relationship between LWR and LWH

Contrarily to common expectations, a significant relationship between LWR and LWH was not found, regardless of the droplet volume used to determine these traits. It is intuitively expected that in highly non-wettable leaves (high LWH), water droplets should roll off more easily (low LWR). This negative correlation was corroborated in some studies

(Brewer and Smith 1997, Brewer and Nuñez 2007), but not in others, where the opposite pattern was found (Pandey and Nagar 2003, Holder 2012). This highlights that the relationship between these traits is still a controversial issue in the literature.

It has been theoretically proposed (McHale et al. 2004), and then verified on synthetic surfaces (Pierce et al. 2008), that the adhesion of liquid drops to solids is not dictated by the static contact angles (hydrophobicity), but by the hysteresis contact angle. Hysteresis is defined as the difference between the maximum advancing contact angle (θ max) and the minimum receding contact angle (θ min) measured on a droplet immediately before it starts moving on a tilted plane. The smaller the contact angle hysteresis, the more easily a drop will roll off the surface (Krasovitski and Marmur 2005). The hysteresis angles are largely influenced by the presence of chemical contaminations, solutes in the liquid or a previous film on the surface, and by the degree of surface heterogeneity (de Gennes 1985), which, in leaves, is mostly created by cuticle wax structures and/or trichomes (Wagner et al. 2003). In leaves with low structural complexity and density of epidermal structures, the hysteresis is minimized, resulting in low leaf water retention (Konrad et al. 2012). Lower trichome density is also related to lower leaf hydrophobicity (Brewer et al. 1991). Therefore, the theoretically expected relationship is just the opposite of that in intuitive thoughts, and droplets should roll off more easily (low LWR) from the most wettable leaves (low LWH). Alternatively, the presence of dense trichome arrangements can simultaneously prevent the spread of water droplets and promote a higher adherence onto the leaf surface, resulting in high values for both traits (Brewer and Smith 1994, Holder 2012).

3.2.5.3 Implications of leaf wetness traits for leaf water uptake

The expected correlation between leaf wetness traits and FWU was not found. Thus, at least for the sub-set of species tested, hydrophobicity and retention cannot be used as proxies to predict the ability of a plant to perform FWU. In this study, FWU was assessed through the submergence of the whole leaf in water, so it is reasonable to assume that leaf traits directly related to water absorption (such as the cuticle chemical compostion and the presence of specialized epidermal structures) may be more important for determining foliar uptake than LWR and LWH, as demonstrated by Eller et al. (2013). If the leaf surface is not water permeable, neither a greater spreading nor a greater persistence of the water droplet on the leaf surface will ensure a higher water uptake. However, the absence of a relationship does not necessarily mean that leaf wetness traits should be precluded. Although labelled as 'wetness trait', the functional significance of LWH may be related to other environmental factors such as vapour pressure deficit, solar radiation or ice formation (Jordan et al. 2005, Koch et al. 2006, Aryal and Neuner 2010, Rosado et al. 2010, Eller et al. 2013). In summary, our findings stress that the validation of LWR and LWH must be done before they can be used as proxies (Rosado et al. 2013), not only for FWU, but also for other ecophysiological processes commonly associated with leaf wettability, such as throughfall, gas exchanges, epiphyll colonization, pollution deposition, canopy interception and water storage.

3.2.5.4 Conclusion

Regardless of the environment, most plants are frequently subjected to leaf wetness events (Brewer 1996). Therefore, a high selective pressure to retain or to repel the water droplets on leaf surfaces may be an important, yet still rarely assessed, ecological process. Due to climate change, the frequency, intensity and duration of rain, fog, dew and drought events are likely to be altered worldwide (Collins et al. 2013). How these changes will affect leaf wetness traits, and thus plant water-use strategies, is an interesting question that remains to be elucidated.

Although LWH and LWR are commonly linked to several ecophysiological processes (from the leaf to the ecosystem level), few studies have assessed the actual significance of these twofunctional traits at local, regional and global scales, which impairs the ability to predict plant responses to changes in water availability. Before the validation of a trait for predicting a given process (e.g. FWU) and for properly comparing leaf wetness traits among different species, it is imperative to standardize the methodological approach used to measure these traits and to identify their functional roles. This study clearly showed that water droplet volume does matter when measuring leaf wetness traits. Not only the absolute values, but also the species ranking, were affected by changes in droplet volume. We suggest a standard 5 μL droplet to measure LWH and a 50 μL droplet to determine

LWR, although a 50 µL droplet is not feasible for small-leaf species, and LWR is less consistent than LWH.

3.2.6 Acknowledgements

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3.2.7 Literature cited

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3.2.8 Supplementary Data

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Figure S1 - Differences in leaf water hydrophobicity and retention among the two studied sites, Atlantic Rain Forest and Tropical Mountain Grassland. Table S1 - Mean ±standard deviation leaf water retention (LWR) values for 14 species from the Atlantic Rain Forest and the Tropical Mountain Grassland, RJ, Brazil. Table S2 - Mean ± standard deviationleaf water hydrophobicity (LWH) values for 14 species from the Atlantic Rain Forest and the Tropical Mountain Grassland, RJ, Brazil.

CONSIDERAÇÕES FINAIS

> Don’t let what you can’t do stop you from doing what you can do.
>
> *John Wooden*

Os resultados deste estudo contribuíram para o entendimento de uma das questões fundamentais da Ecologia, que é determinar os mecanismos subjacentes à estabilidade dos sistemas biológicos (Sutherlandet al. 2013). Experimentos de manipulação de chuva, realizados em várias vegetações campestres ao redor do globo, forneceram um valioso conjunto de dados para se avaliar a importância relativa de diferentes conjuntos de fatores na variação da estabilidade. A falta de padronização metodológica entre os experimentos, considerada até então um dos principais empecilhos para a identificação de padrões e mecanismos gerais de resposta (Hoover et al. 2018, Knapp et al. 2017), foi superada através do uso de ferramentas da meta-análise e de índices padronizados de intensidade de seca; e acabou se mostrando uma vantagem, possibilitando a comparação da estabilidade entre vegetações com uma ampla variação de características abióticas (MAT, MAP, sazonalidade da precipitação e altitude) e submetidas a distintos tipos de seca (intensidade, duração e frequência). Deste modo, observou-se que enquanto a variação na resiliência pode ser explicada pela duração da seca (secas mais longas resultam em menor resiliência) (Parte 1, Figura 5c); variações na resistência e recuperação independem das características da seca e de fatores abióticos (Parte 1, Figura 5a-b). Logo, sugere-se que elas podem refletir diferenças em características do solo e/ou nas características bióticas do sistema. Futuros estudos devem, portanto, fornecer informações mais detalhadas sobre as características bióticas do sistema avaliado, de modo que se possa mensurar a sua importância relativa para a determinação da estabilidade. Caso a importância das características bióticas se confirme, isso implicaria que apenas o uso de fatores climáticos/abióticos não seria suficiente para se prever como as vegetações irão responder aos novos regimes de precipitação. Para se obter uma previsão mais realista, seria necessário incluir os fatores bióticos; e, nesse sentido, a abordagem funcional se apresenta como uma ferramenta útil para promover a melhoria dos modelos de previsão.

A utilidade da abordagem funcional foi demonstrada na Parte 2, através da proposição e aplicação de uma nova abordagem (Parte 2, Figura 1), integrando estratégias eco-fisiológicas e índices de originalidade funcional, o qual permitiu predizer os efeitos da seca sobre a vegetação de Campos de Altitude. Assim, apesar das vegetações montanhosas serem consideradas, de modo geral, como altamente vulneráveis às mudanças climáticas (Assis e de Mattos 2016, Beniston 2003), os resultados deste estudo sugerem uma relativa estabilidade dos Campos de Altitude em resposta à seca (Parte 2, Figuras3-4). Essa estabilidade seria gerada pelo efeito combinado da originalidade (efeito de complementariedade) e redundância funcional (efeito de seleção) (Oliveret al. 2015, Schmid et al. 2001). Em relação à originalidade, embora a maioria das espécies possuam uma estratégia de tolerância à seca, a comunidade apresentou originalidade funcional, através da co-existência de distintas estratégias de resposta (Parte 2, Figura 2b). Isto é, as espécies exibiram maneiras complementares de obter e utilizar a água, e de lidar com a sua escassez. Já o efeito de seleção se daria pela presença de duas espécies co-dominantes (*C. modesta* e *M. ensifolia*) que exibiram uma estratégia CS-escape-evitadora (Figura 2, Parte 2a-b). Ao exibirem características tanto de competidoras, quanto de tolerantes ao estresse; e ao lidarem com a desidratação tanto por meio do escape, quanto pela evitação, elas poderiam responder favoravelmente a diferentes tipos de secas, assegurando assim a estabilidade da comunidade. O grupo funcional ao qual elas pertencem também incluiu espécies subordinadas, resultando numa redundância funcional de resposta (Parte 2, Figura 2b). Porém, a redundância funcional capaz de promover estabilidade somente se daria pela redundância nas características de efeito, mas dissimilaridade na resposta (Introdução, Figura 2d-e). Portanto, sugere-se que futuros trabalhos aperfeiçoem a abordagem aqui proposta, através da inclusão de características de efeito e da avaliação do grau de sobreposição entre grupos de efeito e de resposta (Lavorel e Garnier 2002, Suding et al. 2008).

Nessa abordagem as estratégias de resposta foram descritas por meio do uso simultâneo de características econômicas, hidráulicas e regenerativas, o que contribuiu ao debate se essas características constituiriam eixos distintos de variação (Li et al. 2015,Sacket al. 2013), ou se estariam relacionadas entre si através de *trade-offs* (Reich 2014,Volaireet al. 2018). Os resultados corroboraram a segunda proposição, e demonstraram a existência de pelo menos dois *trade-offs* (Parte 2, Figura 2b): (1) resistência *versus* recuperação, como duas estratégias alternativas para se alcançar a resiliência; e (2) armazenamento *versus* absorção de água, como duas estratégias alternativas para se evitar à desidratação. O *trade-off* resistência-recuperação foi observado tanto em escala global (Parte 1, Figura 4a), como localmente para os Campos de Altitude (Parte 2, Figura 2b), e seria, possivelmente, um reflexo da dicotomia entre as estratégias aquisitiva e conservativa de uso dos recursos (Reich2014). Características conservativas conferem resistência, porém restringem a recuperação; enquanto que características aquisitivas favorecem a recuperação, mas restingrem a capacidade das espécies resistirem aos distúrbios (Grime 2002). Uma das principais implicações desse *trade-off* seria a impossibilidade de se manejar os sistemas biológicos de modo a assegurar tanto alta resistência, quanto alta recuperação. Qualquer ação que promovesse a resistência do sistema necessariamente reduziria sua capacidade de recuperação, e vice-versa (Donohue et al. 2013). Contudo, há evidências de que algumas vegetações seriam igualmente capazes de resistir e de se recuperar (Zeppel et al. 2014), bem como poderiam haver sistemas altamente sensíveis com baixa resistência e baixa recuperação (Nimmo et al. 2015). As relações entre as diferentes propriedades da estabilidade precisam, portanto, ser melhor investigadas, de modo a esclarecer como os *trade-offs* que se estabelecem no nível de indivíduo/espécie podem influenciar na escala de comunidade/ecossistema. Para tanto, futuros estudos devem incorporar o conceito multidimensional de estabilidade; pois,até o momento, tanto os experimentos de manipulação de chuva, quanto as abordagens funcionais, tem dado muito mais enfoque à resistência. A capacidade de recuperação deve ser avaliada nas abordagens experimentais através do monitoramento da comunidade durante o período pós-seca; bem como deve ser incluída nas abordagens funcionais, através da mensuração de características regenerativas (como características das sementes e a capacidade de rebrota, Lavorel 2007, Lavorel e Pausas 2003, Mcintyreet al. 1999), e características hidráulicas relacionadas com a capacidade de reparo de danos após a seca (como capacidade de reparo dos xilemas cavitados, Ogasa et al. 2013).

Já o *trade-off* armazenamento-absorção estabelece que, pelo menos para as plantas dos Campos de Altitude, a estratégia de evitação à desidratação pode ser alcançada ou através do armazenamento de água nas folhas (suculência), ou por meio da absorção foliar de água (FWU) (Parte 2, Figura 2b); mas, não pelos dois mecanismos simultaneamente. FWU também exibiu uma relação negativa com a tolerância ao estresse (Parte 3, Figura 2a-c); logo, as características foliares das espécies tolerantes ao estresse podem dificultar a absorção de água pelas folhas. Por outro lado, as características foliares associadas com a estratégia de ruderalidade resultaram numa maior capacidade para o FWU (Parte 3, Figura 2b-d). Este foi o primeiro estudo a demonstrar a capacidade das plantas dos Campos de Altitude de utilizarem fontes atmosféricas de água como estratégia para lidar com a seca. Em consonância com estudos prévios realizados em outras vegetações (Eller et al. 2016, Gotsch et al. 2015), os resultados aqui obtidos sugerem que as espécies com maior capacidade para FWU representam, justamente, um dos grupos mais sensíveis às reduções na disponibilidade hídrica. Na comunidade de Campos de Altitude, as absorvedoras de neblina já constituem um número reduzido de espécies (baixa diversidade taxonômica e baixa redundância), com baixa frequência na área de estudo, com características funcionais distintas em relação ao restante da comunidade (alta distintividade), e cuja estratégia de resposta à seca (absorção foliar de água) poderá estar comprometida num futuro próximo, em que se prevê uma redução na frequência e na intensidade dos eventos de neblina (Pounds et al. 1999, Still et al. 1999). Assim, a despeito da estabilidade geral dos Campos de Altitude em resposta à seca, a perda desse grupo de espécies pode resultar numa significativa perda de originalidade para a comunidade. Considerando a relação positiva entre estabilidade e diversidade funcional, e o, consequente pressuposto de que se deve conservar o máximo de diversidade para se assegurar o máximo de estabilidade (Pavoine et al. 2005); as espécies absorvedoras de neblina podem, então, ser apontadas como as prioritárias para a conservação nos Campos de Altitude. Uma possível medida de manejo para promover a conservação dessas espécies seria o reflorestamento da vegetação na base das montanhas, o que poderia auxiliar na manutenção dos eventos de neblina em seus topos (Lawton et al. 2001).

Pelo acima exposto conclui-se que as vegetações campestres são resilientes à seca em termos de produção de biomassa; e, devido a existência de um *trade-off* entre estratégias aquisitiva e conservativa de uso dos recursos, a resiliência pode ser alcançada ou através da resistência, ou por meio de recuperação. Consequentemente, espera-se que a diversidade funcional da comunidade influencie navariaçãoda estabilidade entre as vegetações. No caso dos Campos de Altitude, os resultados aqui obtidos sugerem que a resiliência seria alcançada por meio de resistência, dada a predominância de espécies tolerantes à seca (conservativas) nessa comunidade; embora ela apresente também espécies com outras estratégias de resposta. Dentre elas, destaca-se as espécies absorvedoras de neblina, que pode constituir o grupo maissensívelàs reduções na disponibilidade de água. Assim, apesar de resilientes quanto à biomassa, as vegetações campestres podem se mostrar instáveis em termos de diversidade funcional. Num cenário futuro com secas mais intensas, frequentes, duradouras e extremas, o sucesso das estratégias de recuperação pode ficar comprometido, uma vez que ele requer, necessariamente, o retorno às condições originais. Consequentemente, as espécies tolerantes (resistentes) poderão acabar suplantando as demais estratégias, levando a uma homogeneização funcional da comunidade. A despeito das centenas de experimentos de manipulação de chuva já realizados, ainda não se sabe ao certo como as diferentes propriedades da estabilidade irão se comportar em resposta aos futuros regimes de precipitação. Haja vista que a maioria desses estudos aplicaram eventos de seca dentro dos padrões normais de variabilidade dos sistemas. Para se avançar no conhecimento dos mecanismos que promovem a estabilidade dos sistemas, é necessário que futuros experimentos submetam às vegetações a condições muito mais extremas de precipitação, a ponto, justamente, de desviar esses sistemas do seu estado de equilíbrio (Knapp et al. 2017). Esses experimentos devem ser desenhados de modo a testar a possibilidade desses eventos extremos de seca levarem as vegetações a estados alternativos indesejados (degradados e improdutivos), e de avaliar quais medidas podem ser tomadas no sentido de 'empurrar' esses sistemas de volta ao estado desejado (conservado e produtivo).

A despeito de todo o esforço da comunidade científica, a construção de conhecimento, se processa, infelizmente, numa velocidade muito inferior ao ritmo das mudanças climáticas globais (Maris et al. 2017). Diante disso, '*não se deve deixar o que não se pode fazer impedir de se fazer o que se pode fazer*'. Isto é, o desconhecimento dos mecanismos de resposta às mudanças, não deve ser usado como empecilho para não se interferir nos mecanismos que estão causando a mudança. A estabilidade dos sistemas biológicos difere essencialmente dos sistemas inanimados pela sua adaptabilidade. À medida que respondem a um distúrbio, os componentes dos sistemas biológicos têm a habilidade de modificar sua própria estabilidade e a do sistema em que estão inseridos (Folke et al. 2010); e, consequentemente, a possibilidade de alterar a trajetória desse sistema entre distintos estados de equilíbrio. Os seres humanos, como integrantes desses sistemas detém igualmente essa capacidade de mudança. Se hoje nós somos a causa, direta ou indireta, de todos os problemas decorrentes das mudanças climáticas, nós ainda podemos mudar nosso modo de agir e nos transformarmos na solução. Se o clima pode mudar, por que nós não podemos?

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GLOSSÁRIO

Absorção foliar de água (‘*Foliar water uptake*’ FWU)	Passagem de água (na forma líquida ou gasosa) da atmosfera para o interior da folha. Acredita-se que esse movimento seja passivo e governado por uma diferença de potencial entre a atmosfera saturada de vapor de água e o interior da folha com potenciais hídricos mais negativos (Berryet al. 2018, Rundel 1982). FWU pode ser mensurado como o fluxo de água (FWU$_{flux}$, mg H_2O cm^{-2} hour^{-1}), ou seja, como a quantidade de massa de água absorvida por unidade de área foliar por unidade de tempo; ou como o incremento percentual no conteúdo hídrico da folha (FWU$_{lwc}$, %) (Limm et al. 2009).
Adaptabilidade (‘*Adaptability*’)	Capacidade dos componentes de um sistema influenciarem na sua própria estabilidade (Folke et al. 2010).
Área foliar (‘*Leaf area’* LA)	Área total de um dos lados de uma folha individual, usualmente expressa em mm^2 ou cm^2 (Pérez-Harguindeguy et al. 2013).
Área foliar específica (‘*Specific leaf area’* SLA)	Área da lâmina foliar dividida pela massa seca da folha, usualmente expressa em mm^2 mg^{-1}. Representa o custo de construção de cada unidade de área foliar(Pérez-Harguindeguy et al. 2013).
Campos de Altitude (*Páramos*ou*‘Brazilian high altitude grasslands’*)	Formações herbáceo-arbustivas características dos cumes de montanha do sul e sudeste brasileiro (Safford 1999) e que constituem um dos ecossistemas associados ao bioma Mata Atlântica (Brasil 2008).
Capacidade de rebrota (‘*Resprout ability’* RA)	Capacidade da planta produzir novo caule e /ou folhas após a destruição da maior parte da sua biomassa aérea, através do uso de reservas contidas em tecidos basais e/ou subterrâneos, de modo a assegurar a sua persistência na comunidade após a ocorrência de distúrbios (Moreira et al. 2012).
Características de efeito (‘*Effect traits’*)	Características que determinam o efeito das plantas sobre o funcionamento dos ecossistemas (Lavorel e Garnier 2002).
Características de história de vida da	Classificação das plantas de acordo com o tempo médio de

planta (‘*Plant life history traits’*)	sobrevivência dos indivíduos na ausência de distúrbios. Plantas anuais senescem e morrrem ao final da primeira estação de crescimento; enquanto que as perenes, sobrevivem por três ou mais estações (Pérez-Harguindeguy et al. 2013).
Características de resposta (‘*Response traits’*)	Características associadas com a resposta das plantas aos fatores ambientais, como recursos e distúrbios (Lavorel e Garnier 2002).
Características econômicas (‘*Economic traits’*)	Características relacionadas com a assimilação de carbono (veja espectro foliar econômico).
Características funcionais (‘*Functional traits’*)	Características fenológicas, morfológicas, anatômicas e/ou fisiológicas mensuradas no nível de indivíduo, que estão relacionadas a alguma função, e que tem impactos diretos ou indiretos sobre o sucesso reprodutivo dos organismos (Violle et al. 2007).
Características hidráulicas (‘*Hydraulic traits’*)	Características mecanisticamente relacionadas com o modo como as plantas capturam, transportam e utilizam a água; e que descrevem a capacidade das plantas em tolerar condições de baixa disponibilidade hídrica (Griffin-Nolan et al. 2018).
Características regenerativas (‘*Regenerative traits’*)	Características que refletem a capacidade dos organismos realizarem regeneração sexuada e/ou assexuada, de modo a persistirem na comunidade mesmo após a ocorrência de distúrbios (Pausas e Lavorel 2003).
Cavitação (‘*Cavitation’*)	Processo de formação de bolhas de ar no interior dos vasos de xilema ou traqueídeos (Tyree e Sperry 1989)
Competição (‘*Competition’*)	Tendência de plantas vizinhas utilizarem o mesmo quantum de luz, íon de um nutriente mineral, molécula de água e/ou volume no espaço (Grime1973).
Competidora (‘*Competitor’*)	Espécie com ciclo de vida longo, crescimento rápido e características econômicas foliares que possibilitam a maximização da captação de recursos; e, consequentemente, alta habilidade competitiva em ambientes ricos em recursos e não sujeitos a distúrbios (Grime 1977).
Condição (‘*Condition’*)	Fatores abióticos que variam no tempo e espaço e afetam o desempenho dos organismos (Odum e Barrett 2008).

Condutância estomática (‘*Stomatal conductance’* g_s)	Medida da perda de água por transpiração, controlada pelo grau de fechamento estomático e governada pelo gradiente de pressão de vapor entre os tecidos internos da folha e a atmosfera circundante. Usualmente expressa como a quantidade de moléculas de água perdida por unidade de área foliar, por unidade de tempo (mmol m^{-2} s^{-1}) (Damour et al. 2010).
Conteúdo de massa seca foliar (‘*Leaf dry matter content’* LDMC)	Massa seca da folha dividida pela massa fresca, usualmente expressa em mg g^{-1} (Pérez-Harguindeguy et al. 2013).
Curva pressão volume (‘*Pressure–volume curve’* PV-curve)	Gráfico que relaciona mudanças no potencial hídrico foliar ao longo de um gradiente de conteúdos relativos de água na folha. A partir dessa curva é possível determinar o potencial hídrico foliar no ponto de perda de turgor, além de outras características hidráulicas (Turner 1988).
Déficit de pressão de vapor (‘*Vapor pressure deficit’* VPD)	É a diferença entre a pressão de vapor sob condições ambientes e a pressão de vapor no ponto de saturação para a mesma temperatura (Willet al. 2013). Representa, portanto, uma medida da quantidade de umidade presente na atmosfera.
Demanda conflitante (‘*Trade-off*’)	É um dilema evolucionário por meio do qual uma mudança genética que confere aumento no desempenho reprodutivo sob um conjunto de circustâncias necessariamente envolve a redução no desempenho sob um outro conjunto (Grime e Pierce 2002). Assim, o *trade-off* se estabelece sempre que a adoção de uma estratégia reduz a habilidade/eficiência em se desempenhar uma estratégia alternativa (Bolnicket al. 2003).
Densidade de venação (‘*Venation density’* VD)	Comprimento total de nervuras por unidade de área foliar, geralmente expressa em mm mm^{-2} (Sack e Scoffoni 2013).
Densidade específica do caule (‘*Stemspecific density’* SSD)	Massa seca de uma seção do caule dividido pelo seu volume fresco, usualmente expressa em g cm^{-3}. Representa o custo de produção para cada unidade de volume de caule (Pérez-Harguindeguy et al. 2013).
Densidade estomática *(‘Stomatal density’* SD)	Número de estômatos por unidade de área foliar (Xu e Zhou2008).

Distintividade (‘*Distinctiveness’* DIS)	Propriedade de uma espécie (ou organismo) cujas características são dissimilares em relação aos valores médios da comunidade. A distintividade pode ser mensurada como a distância euclidiana de uma determinada espécie em relação ao centro do espaço funcional (Greniéet al. 2017).
Distúrbio (‘*Disturbance*’)	Qualquer processo potencialmente capaz de mudar a estrutura de um sistema, direta ou indiretamente, através da alteração no ambiente biótico ou abiótico (Connell e Ghedini 2015, Standish et al. 2014). Especificamente no contexto de comunidades vegetais, distúrbio também pode ser definido como a perda parcial ou total de biomassa vegetal, ocasionada for fatores bióticos (herbívoros, patógenos, homem) ou abióticos (vento, geadas, dessecação, fogo) (Grime 1977).
Diversidade funcional (‘*Functional diversity’* FD)	Valor e amplitude das características funcionais, de resposta e de efeito, presentes em uma determinada comunidade (Díaz e Cabido 2001).
Diversidade taxonômica (‘*Taxonomic diversity’*)	Número total de diferentes espécies que ocorrem numa determinada comunidade (Díaz e Cabido 2001).
Embolismo (‘*Embolism*’)	Bloqueio da passagem de água através do vaso de xilema ou traqueídeos devido a presença de bolhas de ar (Tyree e Sperry 1989).
Escape à desidratação (‘*Dehydration escape’*)	Plantas podem escapar da desidratação através de ajustes fenológicos, que lhes possibilitam completar o seu ciclo de vida antes de serem submetidas ao estresse hídrico. A estratégia de escape se baseia, portanto, no sucesso reprodutivo antes da seca e na capacidade das sementes se manterem dormentes no banco de sementes durante o evento de seca (Levitt 1972).
Escleróﬁtas (‘*Sclerophyll plants’*)	Plantas que apresentam folhas pequenas, espessas, densas, longevas e com baixa concentração de nitrogênio, e que são características de ambientes áridos e quentes (Chaves et al. 2002)
Espaço funcional (‘*Functional space’*)	Espaço multidimensional definido por um conjunto de características funcionais; e no qual as espécies são posicionadas

	de acordo com os seus valores para estas características (Mouilott et al. 2013)
Espécies dominantes (‘*Dominant species’*)	Espécies com maior contribuição relativa para a biomassa total da comunidade (Grime 1998).
Espécies subordinadas (‘*Subordinate species’*)	Espécies com menor contribuição relativa para a biomassa total da comunidade (Grime 1998).
Espectro econômico foliar (‘*Leaf economic spectrum’* LES)	Gradiente definido por uma série de demandas conflitantes entre características funcionais econômicas (relacionadas a assimilação de carbono); e que representa um balanço entre o custo de construção da folha versus o potencial de crescimento. O gradiente estabelece num extremo espécies com uma estratégia aquisitiva de recurso, e no outro, espécies com uma estratégia conservativa (Díaz et al. 2015, Wright et al.2004).
Espessura foliar (‘*Leaf thickness’* Lth)	Espessura da lâmina foliar, usualmente expressa em mm (Pérez-Harguindeguy et al. 2013).
Estabilidade (‘*Stability*’)	Este termo pode ter inúmeras definições. Aqui a estabilidade é definida como a capacidade de um sistema persistir num determinado estado de equilíbrio mesmo após ter sido sujeito a um distúrbio (Connell e Ghedine 2015); sendo essa capacidade dependente das propriedades de resiliência, resistência e recuperação (Lloret et al. 2011).
Estratégia (‘*Strategy*’)	Combinação específica de características funcionais que reaparecem amplamente entre espécies ou populações, de modo que os portadores dessa combinação específica exibem similaridades ecológicas entre si (Grime 2002).
Estratégia aquisitiva de recursos (‘*Acquisitive resource-use strategy’*)	Estratégia caracterizada por um crescimento rápido, e pela produção de folhas grandes (maior LA), pouco custosas (alto SLA e baixo LDMC), com alta capacidade fotossintética e curta longevidade (Reich et al. 2003, Reich 2014).
Estratégia conservativa de recursos (‘*Conservative resource-sestrategy’*)	Estratégia caracterizada por um crescimento lento, e pela produção de folhas pequenas (menor LA), custosas (baixo SLA e alto LDMC), com menor capacidade fotossintética e maior

	longevidade (Reichet al. 2003, Reich 2014).
Estresse (‘*Stress*’)	Condições, como limitação de luz, água e nutrientes minerais, que restringem a produção de biomassa nas plantas (Grime 1977).
Estresse hídrico (‘*Water stress’*)	Alteração no funcionamento fisiológico da planta que desvia o sucesso reprodutivo abaixo do estado de referência (planta crescendo sob condições ótimas), sendo causado por uma disponibilidade de água menor do que a demanda necessária para a planta (Volaire et al. 2018).
Evento de molhamento foliar (‘*Leaf-wetting events’*)	Eventos, como neblina, orvalho e chuva, que culminam na deposição de água sobre a superfície foliar (Dawson e Goldsmith 2018).
Evento extremo (‘*Extreme event’*)	Episódios estatisticamente raros (extremo climático) que culminam em respostas biológicas extremas, ou seja, em alterações na estrutura e/ou na função que excedem o padrão normal de variabilidade do sistema e demandam longos períodos de recuperação, ou são irrecuperáveis (Smith 2011).
Evitação à desidratação (‘*Dehydration avoidance’*)	Plantas evitam à desidratação quando são capazes de manter o grau de hidratação dos seus tecidos o mais alto possível, mesmo sob condições de menor disponibilidade de água no ambiente. Isto pode ser alcançado através de mecanismos que minimizam a perda de água (e.g. fechamento estomático); maximizam a sua absorção (e.g. raízes profundas) ou o seu armazenamento (e.g. suculência foliar) (Levitt 1972).
Extremidade da seca (‘*Drought extremeness*’)	Probabilidade de ocorrência de um evento de seca baseado nos registros históricos de precipitação (Vicca et al. 2012).
Fração média da superfície foliar alocada em células guarda (‘*Average fraction of the leaf surface allocated to guard cells*’ Fgc)	Proporção da superfície foliar recoberta por células guarda (i.e. células responsáveis pelos movimentos de abertura e fechamento estomático). Pode ser obtida através do produto entre a densidade estomática e a área media das células guarda (De Boer et al. 2016).
Fração media da superfície foliar alocada para poros estomáticos	Proporção da superfície foliar correspondente aos poros estomáticos (i.e. ostíolos). Pode ser obtida através do produto entre a densidade estomática e a área anatômica máxima do poro

(‘*Average fraction of the leaf surface allocated to stomatal pores*’ Fsp)	estomático.
Geófita (‘*Geophyte*’)	Planta perene cujas gemas vegetativas encontram-se posicionadas abaixo da superfície do solo (Raunkier 1934).
Grupo funcional (‘*Functional group’* FG)	Grupos de espécies que respondem às condições ambientais de forma similar (i.e. grupo funcional de resposta) e/ou que tem efeitos similares sobre os processos ecossistêmicos (i.e. grupo funcional de efeito) (Lavorel e Garnier 2002).
Homogeneização funcional (‘*Functional homogenization’*)	Perda de diversidade funcional (i.e. redução da originalidade funcional de uma comunidade), que pode ter efeitos negativos sobre o funcionamento e produtividade dos sistemas ecológicos, levando a deterioração dos serviços e bens ecossitêmicos (Clavel et al.2011).
Índice padronizado de precipitação-evapotranspiração (‘*Standardized precipitation evapotranspiration index* SPEI)	Constitui uma medida de intensidade dos eventos de seca (déficit hídrico climático), computada como a diferença entre a precipitação e o potencial de evapotranspiração mensal obtidos pelo registro climático histórico (> 50 anos) de uma dada localidade, e padronizados usando uma função de densidade de probabilidade, de modo a possibilitar a comparação entre eventos de seca independentemente da localidade e do clima. O SPEI representa, portanto, o número de desvios padrões pelos quais o balanço hídrico climático difere da média mensal histórica para uma determinada localidade, comvalores positivos/negativos indicando condições mais úmidas/secas do que o normal (Vicente-Serrano et al. 2010).
Iso-anisohidria (‘*Iso-anisohydric’*)	Plantas poderiam exibir um contínuo entre um comportamento isohídrico, caracterizado por uma forte regulação na condutância estomática, de modo a reduzir a perda de água por transpiração (mas também a assimilação de carbono) e manter os potenciais hídricos foliares relativamente constantes mesmo sob condições de menor disponibilidade de água no solo; ou anisohídrico, caracterizado por uma fraca regulação estomática, maior perda de

	água por transpiração (mas manutenção da assimilação de carbono), e, consequentes reduções no potencial hídrico foliar em resposta a menores disponibilidades hídricas (Hochberg et al. 2018, Tardieu e Simonneau 1998).
Originalidade funcional (‘*Functional originality’* FO)	É uma medida de diversidade funcional que indica o grau de raridade das características funcionais exibidas por uma espécie, quando comparada com as características das demais espécies presentes na comunidade (Pavoine et al. 2005).
Potencial de evapotranspiração (‘*Potential evapotranspiration’*)	É uma medida da habilidade da atmosfera em remover água de uma superfície através de processos de evaporação e transpiração, assumindo a ausência de controle sobre o suprimento de água (Abatzoglou et al. 2018).
Potencial hídrico foliar de madrugada (‘*Predawn leaf water potential’* Ψ_{pd},)	Considerando que durante a madrugada o potencial hídrico da planta se equilibra com o do seu substrato, o Ψ_{pd} seria uma medida da quantidade de água disponível para a planta. Contudo, esse equilíbrio nem sempre ocorre, devido a transpiração noturna, a cavitação xilemática e/ou a ocorrência de ajustes osmóticos, que levam a um desacoplamento entre o potencial hídrico da planta e do solo (Donovan et al. 2003).
Potencial hídrico foliar (‘*Leaf water potential’* Ψ_{leaf})	É o potencial de energia da água por unidade de volume relativa com a água pura em condições padrões. O potencial hídrico quantifica a tendência da água se mover de uma área (sistema) para outra devido a osmose, gravidade, pressão mecânica ou capilaridade. O potencial hídrico foliar é utilizado, portanto, como uma medida do status hídrico da planta, sendo em geral expresso em unidade de pressão (MPa), com valores progressivamente mais negativos indicando uma menor disponibilidade de água no sistema (Pérez-Harguindeguy et al. 2013).
Potencial hídrico foliar mínimo sazonal (‘*Minimum seasonal leaf water potential*’ Ψ_{min})	É o menor potencial hídrico foliar de meio dia, medido durante a estação mais seca e quente do ano. Ele é o resultado final do balanço entre a disponibilidade de água no solo, a demanda evaporativa e as características hidráulicas da planta. Quanto menor o Ψ_{min} (mais negativo), maior a tensão a planta pode tolerar

	dentro dos vasos de xilema, sendo ainda capaz de manter suas atividades fisiológicas. Portanto, menores valores de Ψ_{min}, refletem uma maior tolerância à seca (Bhaskar e Ackerly 2006).
Potencial hídrico foliar no ponto de perda de turgor (‘*Leaf water potential at turgor loss point’*Ψ_{tlp})	Representa o potencial hídrico no qual as células vegetais perdem o turgor, e o potencial hídrico se iguala ao potencial osmótico. Reflete a capacidade da planta manter suas funções fisiológicas sob condições de déficit hídrico, quanto menor (mais negativo) o Ψ_{tlp}, maior a resistência à seca (Bartlett et al. 2012).
Precipitação oculta ou horizontal (‘*Fog drip*’)	Ocorre quando as partículas de água suspensas na atmosfera são interceptadas pelas plantas e, em seguida, escoadas para o substrato, aumentando o conteúdo de água disponível nas camadas superficiais do solo (Ewinget al. 2009).
Processo ecossistêmico (‘*Ecosystem processes’*)	Característica intrínseca do ecosistema através do qual o ecossistema mantém a sua integridade. Decomposição, produção de biomassa, ciclagem de nutrientes e fluxos de nutrientes e energia são alguns exemplos de processos ecossistêmicos (Oliver et al. 2015).
Recuperação (‘*Recovery*’ RC)	Uma das propriedades da estabilidade de um sistema, sendo definida como a capacidade do sistema compensar as mudanças ocorridas durante o distúrbio (Van Ruijven e Berendse 2010).
Recurso (‘*Resource*’)	Qualquer elemento consumido (utilizado) pelo organismo, como espaço, nutrientes, água, presas, etc (Odum e Barrett 2008).
Redundância funcional (‘*Functional redundancy’*)	Ocorre devido a existência de espécies que exercem efeitos similares sobre os processos ecossistêmico, mas diferem na sua resposta aos distúrbios (Oliver et al. 2015). A redundância funcional, portanto, pode promover a estabilidade da comunidade em resposta a distúrbios, garantindo a manutenção das funções, a despeito da perda de algumas espécies (Naeem 1998, Walker 1992).
Repelência foliar de água (‘*Leaf water hydrophobicity or repellency*’ LWH)	Reflete o grau de espalhamento da água sobre a superfície foliar. A repelência pode ser medida como o ângulo de contato entre uma gota de água e a superfície foliar. Quanto maior o ângulo de contato, mais esférica a gota de água, e maior a repelência da

	superfície foliar. (Aryal e Neuner 2010, Rosado e Holder 2003).
Resiliência (‘*Resilience*’)	Neste estudo a resiliência é considerada como uma propriedade da estabilidade de um sistema, sendo definida como a capacidade do sistema se manter inalterado após um distúrbio (Van Ruijven e Berendse 2010). Contudo, esse termo pode também ser definido como o tempo necessário para um sistema retornar ao seu estado de equilíbrio após sofrer algum distúrbio (‘*enginiring resilience*’, Pimm1984); ou ainda como a quantidade de distúrbio que um sistema pode absorver antes de mudar para um novo estado de equilíbrio (‘*ecological resilience*’ Holling1973).
Resistência (‘*Resistance*’)	Uma das propriedades da estabilidade de um sistema, definida como capacidade do sistema se manter inalterado durante o distúrbio (Van Ruijven e Berendse 2010).
Retenção foliar de água (‘*Leaf water retention’* LWR)	Reflete o grau de adesão da água sobre a superfície foliar. Retenção pode ser medida como o ângulo de inclinação a partir do qual uma gota de água começa a se mover sobre a superfície foliar. Um menor ângulo de retenção resulta numa maior capacidade das folhas eliminarem a água da sua superfície (Aryal e Neuner 2010, Rosado e Holder 2003).
Ruderal (‘*Ruderal’*)	Espécie com crescimento rápido, ciclo de vida curto e uma estratégia aquisitiva de recursos, que investe principalmente no crescimento reprodutivo (produção de sementes) para assegurar uma rápida recuperação em ambientes potencialmente produtivos, mas frequentemente sujeitos a distúrbios (Grime 1977).
Seca (‘*Drought*’)	Déficit de precipitação (i.e. seca metereológica); ou déficit de água no solo (i.e. seca agrícola); ou discrepância entre o suprimento e a demanda de água para a planta que resulta num estresse hídrico para as plantas, causando limitações hidráulicas ao seu desenvolvimento e sobrevivência (i.e. seca fisiológica) (Dai 2010).
Síndrome de dispersão (‘*Dispersal syndrome’*)	Modo principal de dispersão dos propágulos (anemocórico, zoocórico, hidrocórico ou autocórico) (Pérez-Harguindeguy et al. 2013).
Singularidade (‘*Uniqueness*’ UNI)	Propriedade de uma espécie (ou organismo) que

	possuicaracterísticas únicas, ou seja, não compartilhadas por nenhuma outra espécie dentro da mesma comunidade. Singularidade pode ser mensurada como a distância euclidiana de uma espécie em particular em relação ao seu vizinho mais próximo no espaço funcional (Grenié et al. 2017).
Suculência foliar (‘*Leaf succulence’* SUC)	Conteúdo de água contido em cada unidade de área foliar, geralmente expresso em g m^{-2}. (Kluge e Ting 1978).
Tolerância à desidratação (‘*Dehydration tolerance’*)	Plantas toleram à desidratação quando são capazes de manter as suas funções fisiológicas, até certo grau, mesmo sob menores graus de hidratação dos seus tecidos (Levitt 1972).
Tolerância à dessecação (‘*Desiccation tolerance’*)	Plantas toleram à dessecação quando são capazes de equalizar o conteúdo hídrico foliar em relação à umidade atmosférica ambiente e são também capazes de recobrar as atividades fisiológicas após reidratação, mesmo depois de longos períodos desidratadas (Volaire et al. 2018).
Tolerante ao estresse (‘*Stress tolerator’*)	Organismos com ciclo de vida longo, crescimento lento e com uma estratégia de uso conservativo dos recursos, que lhes possibilita a conservação de processos metabólicos e a sobrevivência sob condições estressantes, a despeito tanto do crescimento vegetativo, quanto do reprodutivo (Grime 1977).
Vulnerabilidade do xilema à cavitação (‘*Xylem hydraulic vulnerability to cavitation’*)	Reflete a propensão do xilema perder funcionalidade durante eventos de seca em decorrência da formação e expansão de bolhas de ar dentro dos seus vasos, as quais bloqueiam o transporte de água (Tyree e Sperry1989).

APÊNDICE - Lista das 76 espécies avaliadas neste estudo, ocorrentes nos Campos de Altitude do Parque Nacional do Itatiaia (Rio de Janeiro, RJ, Brasil)(continua)

Família	Espécie	Háb.	N° HRJ	Data coleta	End.	1	2
Alstroemeriaceae	*Alstroemeria foliosa* Mart. exSchult. &Schult.f.	H	12848	25/02/2017	Brasil	NE	NE
	Alstroemeria isabelleana Herb.	H	12847	27/02/2017	não	NE	NE
Amaryllidaceae	*Hippeastrum morelianum*Lem.	H	12890	26/02/2017	Brasil	VU	NE
Apiaceae	*Eryngium glaziovianum*Urb.	H	12722	28/05/2015	Brasil	DD	NE
Apocynaceae	*Oxypetalum glaziovii* (E.Fourn.) Fontella & Marquete	H	12746	24/10/2015	Brasil	NE	NE
Asteracaee	*Achyrocline satureioides* (Lam.) DC.	H	12736	28/05/2015	não	NE	NE
	Baccharis altimontana G.Heiden et al.	S	12703	29/05/2015	Brasil	NE	NE
	Baccharis brevifolia DC.	A	12705	15/07/2015	Brasil	LC	NE
	Baccharis glaziovii Baker	H	12702	19/07/2015	não	NE	NE
	Baccharis grandimucronata Malag.	A	12713	28/05/2015	Brasil	LC	NE
	*Baccharis itatiaiae*Wawra	A	12709	15/07/2015	Brasil	NE	NE
	Baccharis parvidentata Malag.	A	12704	15/07/2015	Brasil	NE	NE
	Baccharis pseudomyriochepala Malag	A	12708	28/05/2015	Brasil	NE	NE
	Baccharis retusa DC.	A	12840	24/03/2017	Brasil	NE	NE
	Baccharis stylosa Gardner	S	12712	28/05/2015	Brasil	NE	NE
	Baccharis uncinella DC.	A	12839	21/01/2017	Brasil	NE	NE
	Baccharis tarchonanthoides DC.	A	12837	27/03/2017	Brasil	NE	NE
	Chaptalia runcinate Kunth	H	12719	14/07/2015	Brasil	NE	NE
	Chionolaena capitata (Baker) Freire	S	12717	28/05/2015	Brasil	NE	NE
	Gamochaeta purpurea (L.) Cabrera	H	12859	21/01/2017	não	NE	NE
	Graphistylis itatiaiae (Dusén) B. Nord.	S	12836	25/02/2017	Brasil	NE	NE
	Grazielia gaudichaudiana (DC) R.M. King & H. Rob	A	12858	09/12/2015	Brasil	NE	NE
	Hieracium commersonii Monnier	H	12862	24/10/2015	não	NE	NE
	Hypochaeris lutea (Vell.) Britton	H	12833	14/12/2016	NA	NE	NE
	*Leptostelma maximum*D.Don	H	12851	26/07/2015	não	NE	NE
	Leptostelma tweediei (Hook &Arn) DJN Hind & GL Nesom	H	12849	25/02/2017	não	NE	NE
	Mikania camporum B.L. Rob.	H	12889	18/07/2015	Brasil	NE	NE
	Mikania glaziovii Baker	H	12714	18/07/2015	Brasil	NE	NE
	Senecio adamantinus Bong	H	12863	21/01/2017	Brasil	LC	NE
	Senecio nemoralis Dusén	H	12834	25/10/2015	Brasil	NE	NE
	Senecio oleosus Vell.	S	12715	29/05/2015	Brasil	NE	NE
	Stevia camporum Baker	H	12852	25/02/2017	não	LC	NE
	Trixis glaziovii Baker	H	12853	25/02/2017	Brasil	VU	NE
	Symphyopappus reitzii (Cabrera) R.M.King & H.Rob.	S	12749	24/10/2015	Brasil	NE	NE
Bromeliaceae	*Fernseea itatiaiae* (Wawra) Baker	H	12748	24/10/2015	Brasil	EM	NE
Campanulaceae	*Lobelia camporum* Pohl	H	12846	25/02/2017	não	NE	NE

APÊNDICE - Lista das 76 espécies avaliadas neste estudo, ocorrentes nos Campos de Altitude do Parque Nacional do Itatiaia (Rio de Janeiro, RJ, Brasil) (conclusão)

Caryophyllaceae	*Cerastium dicrotrichum* Fenzl ex Rohrb.	H	12844	26/02/2017	não	NE	NE
Cyperaceae	*Machaerina ensifolia* (Boeckeler) T. Koyama	H	12885	21/01/2017	Brasil	NT	NE
Ericaceae	*Agarista hispidula* (DC.) Hook. ex. Nied.	A	12724	28/05/2015	Brasil	NE	NE
	Gaultheria serrata (Vell.) Sleumer ex. Kin.-Gouv.	A	12721	28/05/2015	Brasil	NE	NE
	Gaylussacia amoena Cham.	S	12741	24/10/2015	Brasil	NE	NE
	*Gaylussacia chamissonis*Meisn.	S	12856	24/10/2015	Brasil	NE	NE
	Gaylussacia fasciculata Gardner	S	12887	14/07/2015	Brasil	NE	NE
Eriocaulaceae	*Paepalanthus itatiaiensis*Ruhland	H	12739	24/10/2015	Brasil	NE	NE
Escalloniaceae	*Escallonia laevis* (Vell.) Sleumer	S	12845	21/01/2017	Brasil	NE	NE
Fabaceae	*Lupinus gilbertianus* C.P.Sm	S	12888	26/10/2015	não	NE	NE
	Mimosa itatiaiensis Dusén	S	12750	24/10/2015	Brasil	NE	LC
	Mimosa monticola Dusén	H	12835	14/07/2015	Brasil	NE	NE
Geraniaceae	*Geranium brasiliense*Progel	H	12745	24/10/2015	Brasil	NE	NE
Iridaceae	*Gelasine coerulea* (Vell.) Ravenna	H	12700	19/07/2015	Brasil	NE	NE
	Sisyrinchium alatum Hook.	H	12751	24/10/2015	não	NE	NE
	Sisyrinchium nidulare (Hand. Mazz.) I.M. Johnst.	H	12728	25/07/2015	Brasil	NE	NE
Lamiaceae	*Lepechinia speciosa* (A.St.Hil.exBenth.) Epling	A	12864	20/01/2017	Brasil	NE	NE
Lentibulariaceae	*Utricularia reniformis* A St.-Hill	H	12861	28/02/2017	Brasil	NE	NE
Melastomataceae	*Leandra quinquedentata* (DC.) Cogn.	S	12725	17/07/2015	Brasil	NE	NE
	Pleroma hospita (Schrank et Mart. ex DC.) Triana	A	12710	28/05/2015	Brasil	NE	NE
	*Tibouchina sebastianopolitana*Cogn.	H	12854	25/02/2017	Brasil	NE	NE
Myrtaceae	*Myrceugenia alpigena* (DC.) Landrum	A	12734	09/06/2015	Brasil	LC	NE
Onagraceae	*Fuchsia campos-portoi* Pilg. &Schulze-Menz	S	12742	24/10/2015	Brasil	NE	NE
Orchidaceae	*Pelexia itatiaiae* Schltr.	H	12886	28/02/2017	Brasil	NE	NE
Orobanchaceae	*Esterhazya splendida* J.C.Mikan	S	12711	30/05/2015	não	NE	NE
Oxalidaceae	*Oxalis confertissima* A.St.-Hil.	H	12737	15/07/2015	Brasil	NE	NE
Plantaginaceae	*Plantago australis* Lam.	H	12701	28/07/2015	não	LC	NE
	Plantago guilleminiana Decne	H	12855	21/01/2017	Brasil	LC	NE
Poaceae	*Chascolytrum itatiaiae* (Ekman) Essi, Longhi-Wagner & Souza-Chies	H	12857	26/04/2016	Brasil	NE	NE
	Chusquea pinifolia (Nees) Nees	H	12842	12/03/2017	Brasil	LC	NE
	Cortaderia modesta (Döll.) Hack	H	12843	14/12/2016	Brasil	NE	NE
Polygalaceae	*Polygala brasiliensis* L.	H	12850	21/01/2017	não	LC	NE
	Polygala campestris Gardner	H	12730	19/07/2015	não	NE	NE
Primulaceae	*Myrsine gardneriana* A. DC.	A	12732	25/07/2015	não	NE	NE
Proteaceae	*Roupala montana* Aubl.	A	12841	24/03/2017	não	NE	NE
Rosaceae	*Fragaria vesca* L.	H	12860	28/07/2015	não	NE	NE
Rubiaceae	*Coccocypselum condalia* Pers.	H	12729	14/07/2015	não	NE	NE
	Coccocypselum cordifolium Nees. & Mart.	H	12744	25/10/2015	Brasil	NE	NE
	Galium humile Cham. & Schltdl.	H	12735	28/05/2015	não	LC	NE
Symplocaceae	*Symplocos itatiaiae* Wawra	A	12838	18/07/2015	Brasil	EM	NE

Legenda: Hábito (A – arbustivo; H – herbáceo; S – subarbustivo); N° HRJ (Número de tombo no Herbário da Universidade do Estado do Rio de Janeiro); End. (endemismo segundo o banco de dados REFLORA); Status de ameaça segundo 1.REFLORA (reflora.jbrj.gov.br); 2. IUCN (www.iucnredlist.org): NE – não avaliada; EM – em perigo; LC – pouco preocupante; VU – vulnerável e NT – quase ameaçada. Todas as amostras foram coletadas pelo autor nas proximidades do Posto Marco Antônio Moura Botelho (Marcão) (22° 22.377'S e 44°42.286'O; 2.469 m), na subida para a trilha do Morro do Couto, no Parque Nacional de Itatiaia, Rio de Janeiro, RJ, Brasil.