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REVIEW



Stress-gradient framework for green roofs: Applications for urban agriculture and other ecosystem services

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Abstract

- 1. Green roofs are promoted to contribute to more resilient cities by enhancing urban ecosystem services and food systems. Extensive, low-maintenance green roofs experience frequent environmental stresses, which reduce plant survival and growth. Stress-tolerant plants are therefore used to sustain well-established services, such as building temperature regulation. However, transitioning extensive green roofs to provide other key urban services, such as food production, involves less tolerant plant species. Although facilitation exerted by stress-tolerant species (nurses) has been proposed to improve the performance of stress-intolerant species (protégés) in extensive green roofs, the conditions under which facilitation could occur are not well understood. Therefore, a comprehensive framework is needed that integrates current knowledge on how the performance of protégé species is affected by nurse plants across stress conditions.
- We present a framework for green roof research that results in a linear model that integrates (i) modern trait-environment theory and (ii) facilitation ecology in a refined stress-gradient hypothesis (SGH) originally developed following study of other stressful environments.
- 3. The model makes testable predictions on how phenotypic traits mediate the performance response of protégé species to nurse plants along stress gradients in extensive green roofs. This is not only useful for the analysis of eco-physiological performance measures directly linked with multifunctionality and ecosystem services, but also demographic or 'vital' rates that drive species persistence and plant community maintenance.
- 4. We discuss a range of applications related to key agricultural and ecological questions arising from contemporary extensive green roof research, such as enhancing conditions for crop production, weed management, plant invasions and biodiversity conservation. We also provide guidelines for the generation of appropriate data and for fitting this model using readily available statistical procedures.
- 5. Our framework will allow researchers to assess under which environmental conditions nurse-protégé interactions are feasible. We expect the findings from such

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited. © 2023 The Authors. *Ecological Solutions and Evidence* published by John Wiley & Sons Ltd on behalf of British Ecological Society. research to help develop strategies and guidelines for managing environmental conditions that optimize protégé performances that ultimately affect the delivery of ecosystem services in constructed urban green spaces.

KEYWORDS

extensive green roof, facilitation, functional trait, green infrastructure, nurse-protégé interaction, plant trait, trait-environment relationship, urban green space

1 | INTRODUCTION

Green roofs are promoted worldwide for more resilient cities by contributing to urban ecosystem services (Berardi et al., 2014; Oberndorfer et al., 2007). Notably, ecosystem services provided by green roof infrastructure include stormwater capture (VanWoert et al., 2005), regulation of building temperatures (Santamouris, 2014), mitigation of urban heat islands (Susca et al., 2011), increased biodiversity (Köhler & Ksiazek-Mikenas, 2018; Williams et al., 2014), aesthetic value (Sutton, 2014) and food provisioning (Cristiano et al., 2021; Walters & Stoelzle Midden, 2018). The most common application are 'extensive' green roofs, which can be implemented relatively easily on new or existing buildings because they have very shallow substrates, minimal irrigation and are low maintenance (Maclvor & Lundholm, 2011). These substrate conditions coupled with high temperatures and solar irradiation typical of roof tops render extensive green roofs particularly stressful environments for plant growth, making plant species selection especially important and challenging (Lundholm & Walker, 2018).

Species capable of surviving and growing under stressful conditions (or stress tolerant) are therefore selected by the industry for planting on extensive green roofs (Oberndorfer et al., 2007). By stress, we specifically mean abiotic conditions that limit vegetation productivity, such as high temperatures or low moisture (Grime, 1977). In particular, extensive green roof plant communities are dominated worldwide by a single genus, Sedum (Family: Crassulaceae), a succulent low-growing taxa that has evolved shallow-rooting and drought tolerance to survive in the alpine and rocky meadows where it originates (Clausen, 1966; Gravatt & Martin, 1992). As intended for building sustainability purposes, planted stress-tolerant species ameliorate extreme high temperatures and increase substrate water retention, and consequently could act as 'nurses' for other plants that would otherwise grow less or even not survive (Aguiar et al., 2019; Butler & Orians, 2011; Matsuoka et al., 2019; but see Heim & Lundholm, 2014 who found no clear facilitative effects). Importantly, facilitated stress-intolerant species or 'protégés' (sensu Flores & Jurado, 2003) have the potential to augment and diversify ecosystem services provided (discussed below in more detail) since they are functionally different from nurse species (Maestre et al., 2009). Understanding under which conditions the performance of protégé species can be enhanced by nurse plants is therefore important to transitioning extensive green roofs into fully multifunctional service providers.

First, the successful establishment of protégé species could support urban agriculture. Crops are generally stress-intolerant species, and cultivation may require supplemental irrigation or fertilization, which counters the sustainability principle of extensive green roofs as low-input systems. Crops that are best suited to extensive green roofs would be annuals with edible leaves (e.g. basil, chive) or small fruits (e.g. tomato, bean, cucumber), as they may be relatively less susceptible to extreme environmental conditions (Whittinghill et al., 2013). Nurse plants (e.g. *Sedum*) could therefore further support agricultural productivity and food security by enhancing stressintolerant crop survival during extreme environmental conditions on extensive green roofs (Ahmed et al., 2017).

Besides urban agriculture, other ecosystem services can be improved via nurse-protégé interactions. Increased functional diversity, a common outcome of nurse-protégé interactions, has been found to improve water capture and cooling of extensive green roofs (Lundholm et al., 2010; Maclvor et al., 2018; Vasl et al., 2017). A more efficient use of resources associated with nurse-protégé niche complementarity is also hypothesized to limit invasion by spontaneous species (see Funk et al., 2008), which may help reduce the costs associated with green roof weeding. Furthermore, environmental alterations are thought to be necessary to facilitate colonization of native biodiversity (Lundholm & Richardson, 2010), and these alterations could be provided by nurse plants. Increased richness of protégé species can further exert positive cascading benefits on biodiversity on extensive green roofs, supporting insects (Kyrö et al., 2018; Madre et al., 2013), microorganisms (Hoch et al., 2019), birds (Partridge & Clark, 2018) and bats (Pearce & Walters, 2012).

While there have been advances in our understanding of nurseprotégé interactions on extensive green roofs, little is known regarding how these interactions may be modulated by the wide range of environmental stressors acting on these constrained environments. This knowledge gap can be closed by applying a framework that merges ideas discussed under the stress-gradient hypothesis developed in stressful natural environments (Bertness & Callaway, 1994) with conceptual and analytical tools provided by modern traitenvironment theory (e.g. Webb et al., 2010). The aim of our work is to provide such an analytical framework. First, we review the fundamentals of both ideas, provide definitions and review the current knowledge on stress gradients, plant traits and performance measures relevant to extensive green roof research. Second, we present a quantitative model for a trait-based stress-gradient hypothesis. Testing the predictions of this model will allow researchers to assess which environmental conditions enable nurse-protégé interactions to be feasible. Third, we discuss a range of applications related to key ecological questions arising from contemporary extensive green roof research, such as conservation of native plant communities, plant invasions and weed management, and enhanced conditions for crop production. Despite the potential usefulness of a trait-based stress-gradient framework, it is important to note that there are still no appropriate datasets in the green roof literature that can be contrasted with the predictions that emerge from this framework. We hope that our work will guide the generation of such data.

2 | MERGING THE STRESS-GRADIENT HYPOTHESIS WITH MODERN TRAIT-ENVIRONMENT THEORY

Much of what we know about the environmental controls of plantplant facilitation in stressful natural or seminatural environments, such as drylands, has been motivated and framed by the stressgradient hypothesis (Callaway, 2007; Lortie & Callaway, 2006; Maestre et al., 2009). The stress-gradient hypothesis (SGH) proposes that the effect of neighbouring plants would change from negative (competition) to positive (facilitation) as stress levels increase (Figure 1; Bertness & Callaway, 1994). Further refinements of the SGH proposed that the relationship between interaction sign (facilitation vs. competition) and stress level depends on the type of stress (resource vs. non-resource) and the traits of interacting species (Maestre et al., 2009). This means, for instance, that species with stress-intolerant traits would be more likely to be facilitated than those with stress-tolerant traits; we will discuss in more detail the predictions of the refined SGH (as proposed by Maestre et al., 2009) in the section 'A quantitative model for a refined trait-based stress-gradient hypothesis'.

In turn, modern trait-environment theory provides a comprehensive framework for understanding trait variation along environmental gradients, or trait-environment relationships, and how these relationships affect local community assembly and species distributions (Laughlin & Messier, 2015; Shipley et al., 2016; Vesk, 2013; Webb et al., 2010). We define a trait as a measurable, heritable feature of plants that determines performance (e.g. growth) and overall fitness (Garnier et al., 2016; McGill et al., 2006; Shipley et al., 2016; Violle et al., 2007). This theory emphasizes that trait-environment relationships result from the ecological process of natural selection, where environmental conditions drive a specific trait expression over another depending on the performance conferred by such trait values (Laughlin & Messier, 2015; Shipley, 2010; Shipley et al., 2016; Vellend, 2016; Webb et al., 2010). To test natural selection ideas, this theory proposes the use of linear models that link species' performance to the interaction between species' traits and environmental gradients, or trait-environment interactions (Laughlin & Messier, 2015; Rolhauser et al., 2021; Vesk, 2013; Webb et al., 2010).

Importantly, trait-based facilitation (and competition) can be seen as a special case of natural selection, since plant performance and the outcome of plant-plant interactions are at least



FIGURE 1 Summary of the original stress-gradient hypothesis and its predictions. We express this hypothesis in terms of the relationship between the performance of one or more target plant species (P) and the density of a neighbour species (D), and how this relationship is affected by a stress gradient (S, e.g. decreasing water availability). From top to bottom, the figure connects increasing abiotic stress with the main hypothesis (neighbours become beneficial as stress levels increase) and the basic predictions that D–P relationships should change from negative to positive (graphs with red and blue lines respectively). The bottom graph with orange line shows the resulting positive relationship between stress and the slope of the D–P relationship. Plant drawings created with BioRender.com.

partially dictated by the traits of interacting species (Aarssen, 1989; Keddy, 1992; Rolhauser et al., 2019; Verdú et al., 2021). Therefore, the linear models proposed by modern trait-environment theory can provide a unifying quantitative framework to evaluate predictions of the refined SGH.

Here we focus on the responses of protégé species that may help expand extensive green roof multifunctionality, from native species with conservation value to those cultivated for urban food production. We propose to conceptualize this phenomenon as a chain of effects (Figure 2), where the effects of nurse plants on protégé performance (nurse-protégé interactions; single green arrow in Figure 2) depend on environmental stressors (double brown arrow) and protégé traits (triple blue arrow). We will model this chain of effects as trait-environment interactions that affect protégé performance, as proposed by modern trait-environment theory. Before getting into the details of our model, we will review the current knowledge on stress gradients, plant traits and performance measures relevant to extensive green roof research.

3 | EXTENSIVE GREEN ROOF FEATURES: ENVIRONMENTAL STRESSORS, PLANT TRAITS AND PERFORMANCE MEASURES

3.1 | Environmental stressors

As extensive green roofs are a proposed solution for enhancing urban ecosystem services by greening impervious building exteriors, these are often found in urban areas that experience elevated pollution, urban heat island effects and competition from invasive species. Urban rooftops are generally exposed to intense sunlight, which can directly cause leaf damage and death among sensitive plants (Buckland-Nicks et al., 2016; Getter et al., 2009). High radiation and temperatures further increase evaporation rates that may surpass plant survival thresholds (MacIvor et al., 2011). Wind-mediated transpiration demand can be exacerbated on exposed green roofs. Both high wind speeds and heavy rainfall can cause erosion of substrates from extensive green roofs reducing water-retention capacity (VanWoert et al., 2005; Vo et al., 2012). Additionally, water and nutrient availability are heavily constrained by the nature of extensive green roof substrates, which are often composed by infertile porous materials that promote fast drainage following rain events and meet roof load limits (Hill et al., 2016). The combination of high water demand and low water availability render extensive green roofs extremely stressful, in a similar way to drylands (Dirks et al., 2016).

3.2 | Plant traits

Traits for optimal performance in extensive green roofs have been documented over the last two decades focusing, for instance, on species selection for survival under frequent water deficits (Du et al., 2019) or maximized multifunctionality (Xie et al., 2018). In particular, Lundholm et al. (2015) recommend the use of species with high specific leaf area (SLA), leaf dry matter content, leaf size (LS) and plant height (H) to confer optimal green roof function. These leaf traits align with good trait indicators of the outcome of nurseprotégé interactions in a dryland (Rolhauser & Pucheta, 2016).

Beyond morphological traits, key hydraulic traits, such as leaf hydraulic conductance, leaf water potential, stomatal conductance and subsequent net photosynthesis rates, should provide valuable information in these water-deficit environments. For instance, *Sedum* uses a strategy for drought tolerance via reduced transpiration allowed by CAM photosynthesis (Clausen, 1966). On the other hand, grasses absorb water and have high transpiration rates, thus quickly drying out substrates (Compton & Whitlow, 2006), allowing the green roof substrate to absorb more water in the following rain event (Maclvor et al., 2011). Furthermore, in green roofs with edible species used for crop production and urban food systems, chemical traits such as levels of macro-nutrients, micro-nutrients and secondary metabolites, are other important plant traits on green roofs (Ahmed et al., 2017; Walters & Stoelzle Midden, 2018).

While research exists on plant communities and plant traits for successful extensive green roofs, much of this work is at the aboveground scale. Root functional traits are largely the interface between water stressed substrates and plant survival and have been used to empirically describe root response to localized soil chemical resources including macro- and micro-nutrients (Borden et al., 2019), soil moisture regimes (Fort et al., 2017) and multiple soil physical properties (Borden et al., 2020). Root traits respond to resource gradients in substrate by, for instance, increasing the absorptive roots' surface to enhance uptake capacity (Isaac et al., 2021) This root plasticity is in part due to signals from the rooting environment (Miner et al., 2005). As a result, root traits, such as specific root length, can be used as indicators of plants' strategies in extensive green roof systems (Chu & Farrell, 2022).

3.3 | Plant performance measures

We define performance as a process measurable on plants or groups of plants across time, therefore it is usually more susceptible to measurement timeframes than traits. Generally, performance is the variable of interest for practitioners, that is, the process that is sought to be maximized or optimized. Plant performance can be framed from both demographic (as in Violle et al., 2007) and ecophysiological (as in McGill et al., 2006) perspectives (Figure 2). A species' 'demographic performance' refers to demographic transitions (also known as 'vital rates' or 'fitness components') such as growth, survival and fecundity that ultimately affect population fitness, the latter being the growth rate of a population in a given place (Laughlin et al., 2020; Violle et al., 2007). Therefore, demographic performance is most relevant for community assembly and maintenance (Figure 2). Local population size can be used as a proxy of fitness assuming that dispersal is relatively unimportant (Shipley et al., 2016)



FIGURE 2 Conceptual influence diagram (from top of the figure to bottom) showing the effects of nurse plants (green single-lined arrow), environmental stressors (brown double-lined arrow) and protégé traits (blue triple-lined arrow) on the performance of protégé species in extensive green roofs, as proposed by a refined trait-based stress-gradient hypothesis. Collate symbols mean that one variable modifies the effect of another (i.e. a mathematical interaction), for instance, environmental stressors affect the relationship between nurse and protégé plants. Protégé performance can be measured at a demographic level or at an eco-physiological level. Species demographic performances affect community dynamics, while eco-physiological performances affect ecosystem processes and services (pink arrows). Eco-physiological performances may also affect community dynamics via their effect on demographic performances, although the link between eco-physiology and demography is not shown in the figure. Ecosystem processes also depend on community dynamics (orange arrow). Examples and subdivisions of each type of variable are shown with bullet points. See details on definitions and examples in section on 'Extensive green roof features'. *Setaria*, bean and snapdragon drawings created with BioRender.com. Picture of extensive green roof by Ken Jones from www. utoronto.ca/news.

or not strongly correlated with (or confounded by) the traits involved in the analysis (Rolhauser et al., 2021).

A species' 'eco-physiological performance' refers to the acquisition and allocation of energy and nutrients, such as sunlight interception and photosynthesis (McGill et al., 2006). Eco-physiological performances have dual effects. First, they affect demographic performances (Geber & Griffen, 2003) by determining energy budget surpluses available for species (McGill et al., 2006). Second, ecophysiological performances relate to ecosystem processes (energy flow and chemical cycling) and the associated services (Figure 2) due to their direct link with environmental conditions (Garnier et al., 2016). Net primary productivity (or plant biomass productivity), litter decomposability, nitrogen fixation and retention, nitrogen use efficiency and water use efficiency are generally important species eco-physiological performances (Garnier et al., 2016). Absorption of domestic wastewater pollutants, such as phosphate and nitrate (Liu et al., 2021), and pollen and nectar production (Maclvor et al., 2015) are examples of eco-physiological performances that are additionally important for extensive green roofs. An eco-physiological performance measure may not affect demographic performance and ecosystem functioning equally. For instance, litter decomposability may be directly related to nutrient cycling but its link to demographic performance may be less straightforward. Importantly, whether an eco-physiological performance is conceived of as a trait (e.g. water use efficiency) would depend on the research question (Geber & Griffen, 2003).

The distinction between demographic and eco-physiological performance accommodates often disparate research agendas: one focused on community dynamics (i.e. assembly, stability, succession, invasion, disassembly) and another on ecosystem services. Nonetheless, these phenomena are highly related since the sustainability of ecosystems services would depend on the stability of community structure in green roof systems (Figure 2).

4 | A QUANTITATIVE MODEL FOR A REFINED TRAIT-BASED STRESS-GRADIENT HYPOTHESIS

4.1 | Theory

Studying interactions between individuals requires analysing the relationship between the individual performance of target species (protégé species in our case) and the density of neighbours (nurse species in our case; Freckleton & Watkinson, 2000; Keddy, 1989; Lortie et al., 2016). The slope of these 'density-performance relationships' (Figure 1) can be used as a single measure of interaction strength, often referred to as the 'interaction coefficient' (Abrams, 2001). That is, negative density-performance relationships would indicate competitive effects of nurses on protégé, whereas positive relationships would indicate facilitation.

The SGH in its initial form (Bertness & Callaway, 1994) predicts that interaction coefficients should change from negative to positive as stress levels increase, determining a positive 'stress-interaction relationship' (Figure 1). However, according to the refined SGH (Maestre et al., 2009), this prediction would only hold when stress is caused by a non-resource factor, such as temperature. On the other hand, an n-shaped (or hump-shaped) stress-interaction relationship should be expected when the stress gradient is driven by a resource, such as soil water. This n-shaped stress-interaction relationship would be the result of competition regaining importance under high stress, where stress amelioration on protégé species does not compensate resource consumption by nurse species (Holmgren & Scheffer, 2010; Maestre et al., 2009; Michalet et al., 2006).

Furthermore, acquisitive or stress-intolerant protégé species tend to be more intensely facilitated leading to steeper stress-interaction relationships when compared to conservative or stress-tolerant protégés (Maestre et al., 2009; Michalet et al., 2006). A conservation-acquisition (or 'slow-fast') continuum can be directly characterized using economic traits such as SLA and specific root volume (SRV), the inverse of root tissue density (Bergmann et al., 2020; Reich, 2014). These trait-based mechanisms of plant-plant interactions mean that protégé traits can affect stress-interaction relationships (Figure 2). As suggested by trait-environment theory, the chain of effects depicted in Figure 2 can be modelled as a three-way interaction effect of nurse plants, environmental stressors and protégé traits on protégé performance, as explained below.

4.2 | The model

Our model links the performance (*P*) of individuals of protégé species *i* in location *j* to the mathematical interaction between a trait (*T*) that characterizes the individuals of protégé species *i*, and nurseplant density (*D*) and stress level (*S*) that characterize location *j* where protégé individuals coexist (locations *j* can be experimental plots or whole green roofs depending on the research question). This is a particular case of trait–environment model where nurse-plant density is considered as an environmental gradient. As an example, we assume that trait (T_i) is positively related to resource acquisition in environments subjected to drought stress, such as specific root volume, or SRV (Rolhauser & Pucheta, 2016). We account for nonlinearities in functional relationships using quadratic terms, and all variables (T_i , D_i and S_i) are thought to be centred to zero. The model is:

$$\begin{aligned} P_{ij} &= \beta_0 + \beta_1 D_i + \beta_2 D_i^2 + \beta_3 S_j + \beta_4 S_j^2 + \beta_5 D_j S_j + \beta_6 D_j S_j^2 + \beta_7 D_j^2 S_j \\ &+ \beta_8 T_i + \beta_9 T_i^2 + \beta_{10} D_j T_i + \beta_{11} D_j^2 T_i + \beta_{12} D_j T_i^2 + \beta_{13} S_j T_i + \beta_{14} T S_j^2 i \\ &+ \beta_{15} S_j T_i^2 + \beta_{16} D_j S_j T_i \end{aligned}$$
(1a)

The first parameter, β_0 , is an overall y-intercept. Furthermore, since D_i is centred at zero, β_1 measures the overall direction (positive or negative) and strength of nurse-plant density effect on protégé performance (Aiken et al., 1991; Schielzeth, 2010), that is, the mean slope of the density-performance relationship. β_2 measures the mean curvature of the density-performance relationship; negative values of β_2 indicate nshaped relationships and positive values indicate u-shaped relationships. Similarly, β_3 and β_4 measure the mean slope and curvature of the stressperformance relationship, while β_{o} and β_{o} measure the mean slope and curvature of the trait-performance relationship (Rolhauser et al., 2019; Rolhauser & Pucheta, 2017). Parameters β_5 , β_6 and β_7 are density-stress interactions, β_{10} , β_{11} and β_{12} are density-trait interactions and β_{13} , β_{14} and $\beta_{\rm 15}$ are stress-trait interactions, while $\beta_{\rm 16}$ is the three-way interaction. To focus on density-performance relationships (as functional descriptors of interaction strength), Equation (1a) is rearranged to gather terms for the mean effect of the nurse-plant density D_i on P_{ii} , yielding:

$$P_{ij} = D_i \left(\beta_1 + \beta_5 S_j + \beta_6 S_j^2 + \beta_{10} T_i + \beta_{12} T_i^2 + \beta_{16} S_j T_i \right) + \beta_0 + \beta_2 D_i^2 + \beta_3 S_j + \beta_4 S_j^2 + \beta_7 D_j^2 S_j + \beta_8 T_i + \beta_9 T_i^2 + \beta_{11} D_j^2 T_i + \beta_{13} S_j T_i + \beta_{14} S_i^2 T_i + \beta_{15} S_i T_i^2$$
(1b)

Then, the trait- and stress-dependent mean slope of the densityperformance relationship is:

Mean slope of D – P relationship = $\beta_1 + \beta_{10}T_i + \beta_{12}T_i^2 + S_j(\beta_5 + \beta_{16}T_i) + \beta_6S_j^2$ (2)

Equation (2) reflects a stress-interaction relationship, where $\beta_1 + \beta_{10}T_i + \beta_{12}T_i^2$ is a trait-dependent y-intercept, while $\beta_5 + \beta_{16}T_i$ measures the mean slope and β_6 the curvature of this relationship.

4.3 | Model predictions

Our model reproduces the n-shaped stress-interaction relationships expected for resource-driven stress gradients by the refined SGH when parameter β_6 is negative and relatively large (Figure 3). The stress-interaction relationship of the acquisitive species (e.g. high SRV) is 'higher' compared to the conservative species, reflecting the higher sensitivity of the former to stress amelioration (Figure 3b). This difference between species is captured by parameter β_{10} (set to 0.2), which measures the effect of T_i on the y-intercept of stressinteraction relationships (β_{12} would also affect the y-intercept but was set to zero for simplicity; Figure 3a). The higher sensitivity to stress of the acquisitive species also determines that the peak of facilitation for this species occurs at lower resource-driven stress levels compared to the conservative species (Figure 3b). This shift is captured by the trait-dependent component of the mean slope of the curve, β_{16} , which was set to a negative value (-0.2) meaning that nurse-plant effects tend to shift from positive to negative as resource acquisitiveness of protégé species (T_i) increases. Parameter β_5 affects the slope of stress-interaction relationships for all species alike and was set to -0.5 so that $\beta_5 + \beta_{16}T_i$ is nearly zero for the conservative species (i.e. -0.5 -0.2(-2)=-0.1) and more clearly negative for the acquisitive species (i.e. -0.5 -0.2(2)=-0.9; Figure 3a). This difference between species is due to the higher sensitivity of the acquisitive species to increased stress compared to a stress-tolerant species, as suggested by the refined SGH (see table 1 in Maestre et al., 2009).

The model also reproduces the monotonic relationships predicted by the refined SGH for non-resource gradients (Figure 3c,d). Parameter β_6 is set to a small value (-0.1) to limit the curvature of the relationships. The stress-interaction relationship of the acquisitive species has both higher y-intercept and slope compared to the relationship of the



FIGURE 3 Predictions according to Equation (2), which are consistent with a refined trait-based stress-gradient hypothesis. The interaction surface (a) shows the relationship between nurse-plant effects on the performance of protégé species (quantified as the mean slope of the density-performance relationship) and the mathematical interaction between a trait characterizing protégé species and a gradient of abiotic stress driven by a resource (e.g. available water). The trait is thought to be positively related to resource acquisition (e.g. specific root volume). Yellow and red lines show stress-interaction relationships for species with conservative (or stress tolerant; trait value = -2) and acquisitive (or stress intolerant; trait value = 2) strategies respectively. Panel (b) features these stress-interaction relationships in a two-dimensional plot. Panels (c and d) are the same as (a and b), respectively, but for a gradient of abiotic stress driven by a non-resource or regulator (e.g. temperature). In this case, the trait is thought to be positively related to temperature sensitivity (e.g. leaf size). Values for relevant parameters (Equation 2) are in blue above each interaction surface.

conservative species, reflecting the higher sensitivity of the former to non-resource stress (Figure 3c,d). These differences are captured by the trait-dependent components in the y-intercept (β_{10}) and the slope (β_{16}) of stress-interaction relationships, which in this case are both positive (while β_{12} was set to zero for simplicity; Figure 3c).

Fitting model 3 to data from observational or manipulative experiments could be completed using generalized linear models (GLM; Brown et al., 2014; Warton et al., 2015), generalized linear mixed models (GLMM; Jamil et al., 2013; ter Braak, 2019) and Bayesian GLMM (Ovaskainen & Abrego, 2020; Ovaskainen et al., 2017). These generalized models can accommodate many different probability distributions for the response variables, such as continuous nonnegative (e.g. growth), proportions (e.g. survival) and counts (e.g. density). From these models, the frequentist GLMM approach seems to offer the best balance between model flexibility and ease of use (ter Braak, 2019).

5 | APPLICATIONS AND PRACTICAL CONSIDERATIONS

Our model can be applied to assess several research questions that can be classified under two related agendas: community dynamics and ecosystem services (Figure 2). Community dynamics are directly relevant for green roof plant biodiversity conservation and weed management. For instance, those interested in plant biodiversity conservation may want to ask to what extent do nurse-protégé interactions contribute to the establishment of native vegetation on extensive green roofs. As a first step, researchers may opt for a community-level observational approach, where the abundance (ideally, density, as a proxy of fitness) of each spontaneous native plant species (i) is recorded across several extensive green roofs (i.e. each green roof would be a location i). Preferably, trait values of protégé species should be measured within each location (j), although mean values extracted from databases (e.g. TRY, www.try-db.org; Kattge et al., 2011) can also be used. Surveyed green roofs should differ in stress levels (e.g. available water, temperature, wind exposure) and in the density of a stress-tolerant nurse species (e.g. Sedum species). Ideally, these two gradients should be orthogonal to avoid inference problems, although orthogonality may be difficult to find given that stress levels may affect nurse-plant density.

Lack of orthogonality between nurse-plant density and stress can be solved by manipulating nurse-plant density within each green roof, generating a density gradient or, in case of logistic limitations, a binary design (e.g. with and without nurse plants). A fully manipulative study can also be adopted where all relevant gradients are fixed by researchers including stress (e.g. water availability), nurse-plant density (e.g. *Sedum*) and protégé traits (e.g. SLA of native species). In this case, the experimental plots would be locations *j* in our model and could be arranged in a single green roof.

In all cases above, the abundance of native species can be modelled as the response variable following Equations (1a) and (1b). Abundance and density are nonnegative variables that are best modelled using a GLM(M) assuming the appropriate distribution (e.g. negative binomial for density data). Random effects can be used in a GLMM to accommodate hierarchical structures of data, such as in the case where nurse-plant density is nested within stress levels. GLMMs have already been used for similar purposes in natural environments, for instance, explaining nearly 40% of variation in the abundance of 185 herbaceous species distributed among 189 forested sites (Rolhauser et al., 2021).

A similar community-level approach can be taken to study the dynamics of weed communities in extensive green roofs. Nonetheless, researchers may want to focus on particularly problematic invasive species, as is frequent in the field of biological invasions (Gurevitch et al., 2011). In these cases, rather than abundance, more detailed measures of demographic performance of invasive species can be used that directly or indirectly relate to fitness, such as survival, growth or germination (Carmona-Crocco et al., 2020; Shipley et al., 2016; Violle et al., 2007). Measures of eco-physiological performance related to demographic performance, such as photosynthetic rate or water acquisition, can also be studied to better understand mechanistic links with the environment (McGill et al., 2006). In such population-level studies, it is essential to measure the traits of the invasive protégé species in each location (rather than extracting a mean value form a database) since within-species variation would be unavoidably necessary in these cases.

Researchers may also be interested in understanding and predicting under which environmental conditions does facilitation feasibly enhance ecosystem services mediated by the ecophysiological activity of protégé species on extensive green roofs. As discussed in previous sections, a wide range of eco-physiological performances may be of interest. If the objective is to use nurseprotégé interactions to improve urban food systems, accumulated plant biomass could be modelled as a function of nurse-plant density and relevant stress gradients and protégé traits, for example, water demand and leaf nutrient concentration respectively. This analysis would indicate (i) whether and under which water-demand conditions the crop is facilitated (or competed) by the nurse species, (ii) how much nutrient can be harvested per unit of area (biomass×nutrient concentration) and, importantly, (iii) whether the yield of facilitated plants (i.e. under relatively high stress) compares with the yield of isolated plants (i.e. without nurses) in more benign conditions. The comparison in this last point would be key to assess whether crop production in a stress-plus-nurse environment is feasible or whether irrigation needs to be added (and nurses be removed), in which case the associated environmental and economic costs should be evaluated.

6 | CONCLUSIONS AND IMPLICATIONS

In this article, we present a framework that integrates the analytical machinery of modern trait-environment theory with facilitation ecology embodied in the stress-gradient hypothesis to make predictions on how phenotypic traits mediate the response of extensive green roof plant species to the presence of nurse plants. Both modern trait-environment theory and the stress-gradient hypothesis have separately received considerable attention. However, comprehensive models that merge both phenomena have yet to be fully defined and fitted to data, with clear applications to the applied fields of urban agriculture and green infrastructure research but also within more basic research focused on natural stressful environments.

Specifically, by quantifying the trait-stress-nurse chain of effects on protégé performance (Figure 2) through an output such as Figure 3, researchers will be able to assess which portion of the stress gradient will favour positive nurse-protégé interactions and which conditions will generate competition. Nonetheless, it is important to note that maximizing facilitation does not mean maximizing plant performance in absolute terms. That is, nurses may increase protégé performance under intermediate or high stress, but this performance may be significantly lower compared to a situation with both low stress and low interspecific competition. This is particularly important for food-production purposes, where economic and environmental criteria need to be considered in terms of yield and necessity of external resources. A similar reasoning can be applied to conservation purposes: what is better for maximizing plant diversity on extensive green roofs, using nurse plants to ameliorate stressful conditions or supplementing limiting resources via external sources, such as irrigation? Our framework coupled with studies on the impact of alternative management scenarios can help answer these kinds of important questions.

Emerging research on green roofs requires novel approaches to assess a suite of constraints and stressors. Overall, our analytical framework promotes a better understanding of the plant species and communities prescribed to extensive green roofs and other constructed green infrastructure where urban environmental stressors influence plant interactions, impacting plant performance and, consequently, ecosystem services. Ultimately, we expect the application of this framework to lead to research findings that can be applied to develop evidence-based strategies and guidelines for managing environmental conditions on green roofs that optimize protégé performances for increased and more diversified ecosystem service delivery.

AUTHOR CONTRIBUTIONS

Andres G. Rolhauser was involved in conceptualization, methodology and writing—original draft, review and editing. J. Scott Maclvor, Adriano Roberto and Selena Ahmed were involved in writing—review and editing. Marney E. Isaac was involved in conceptualization and writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

J. Scott Maclvor is an Associate Editor of *Ecological Solutions and Evidence*, but took no part in the peer review and decision-making processes for this paper. The authors declare no other conflict of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable here as no data were generated or analysed in this study.

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