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RESEARCH ARTICLE

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Biodiversity effects on grape quality depend on variety and management intensity

Magdalena Steiner[1] | James B. Grace[2] | Sven Bacher[1]

[1]Ecology and Evolution, Department of Biology, University of Fribourg, Fribourg, Switzerland

[2]US Geological Survey, Wetland and Aquatic Research Center, Lafayette, LA, USA

Correspondence
Magdalena Steiner
Email: magdalena.steiner1@hotmail.com

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Abstract

1. Interactions between plants can be beneficial, detrimental or neutral. In agricultural systems, competition between crop and spontaneous vegetation is a major concern. We evaluated the relative support for three non-exclusive ecological hypotheses about interactions between crop and spontaneous plants based on competition, complementarity or facilitation.
2. The study was conducted in Swiss vineyards with different vegetation management intensities. In all, 33 vineyards planted with two different grape varieties were studied over 3 years to determine whether low-intensity vegetation management might provide benefits for grape quality parameters. Management intensity varied with the degree of control of spontaneous inter-row vegetation. Features of spontaneous vegetation measured included total cover, total species richness and abundance of nitrogen-fixing plants. Grape quality parameters of known importance to wine making (yeast assimilable nitrogen, sugars, tartaric acid and malic acid) were determined by Fourier-transform infrared spectroscopy (FTIR). Using structural equation modelling, we evaluated hypotheses about the multivariate responses of grape quality parameters as well as the direct and indirect (plant-mediated) effects of management.
3. Observed effects of management differed between grape varieties. Management intensity and abundance of N-fixing plants significantly influenced grape quality parameters while total richness of spontaneous plants did not have detectable effects. Abundance of N-fixing plants was enhanced by low-intensity management resulting in increased N content in the red grape variety *Pinot noir*, potentially enhancing grape quality, while measured soil N content did not explain the increase.
4. *Synthesis and applications*. Our study shows that crop quality can be enhanced by spontaneous plants, in this case by the abundance of a key functional group (N-fixers), most likely through plant–plant or plant–microbe facilitation. However, beneficial interactions may have a high specificity in terms of facilitation partners and may have contrasting effects at low taxonomic resolutions such as crop varieties. Generally, increasing plant biodiversity in agricultural systems may increase competition with

James B. Grace and Sven Bacher shared senior authorship

crops. Thus, the identification of suitable interaction partners and a careful balance between crop variety and spontaneous plant species may be necessary to utilize beneficial interactions and to reduce the trade-off between agricultural production and biodiversity to achieve a sustainable ecological benefit in agricultural systems.

KEYWORDS

competition, complementarity, ecological intensification, facilitation, grape quality, N-fixing plants, spontaneous vegetation, vineyards

1 | INTRODUCTION

Understanding the complex dynamics of multifactorial biological systems is crucial for the development of more sustainable agricultural practices. A central question is whether the benefits of biodiversity found in natural systems can be applied to agroecological practices. The answer to that question can be expected to depend on the precise mechanisms whereby elements of biodiversity influence the desired outcomes in agricultural systems (Halford et al., 2015).

Competition for resources is probably the best-known interspecific interaction resulting in a negative covariance and reciprocal disadvantages for the involved organisms, but not necessarily for system functioning (Tilman, 1994, 1999, 2000). Niche-efficiency theory (Liang et al., 2015) predicts that a higher plant diversity enhances complementarity effects, based on niche differentiation and resource partitioning (Loreau & Hector, 2001; Loreau et al., 2001), and could therefore promote plant productivity due to reduced competition. Another type of species interaction is facilitation, where the presence of one plant species is beneficial for another (Loreau & Hector, 2001). Facilitation can be based on different mechanisms. In succession processes, pioneer plants increase the favourability of the microhabitats and thus, facilitate the colonization of following plants (Connell & Slatyer, 1977; Gómez-Brandón et al., 2010). Facilitation can occur between plants directly, where root exudates directly increase the bioavailability of nutrients, or indirectly, for example, mediated by micro-organisms (Berg & Smalla, 2009). Initial research on plant–plant facilitation was mostly focused on degraded or stressful environments such as deserts or salty habitats (Brooker et al., 2008; Callaway & Pennings, 2000; Gómez-Brandón et al., 2010; He & Bertness, 2014). More recent studies have explored how facilitation can also operate in productive environments. Suggestions for the direct application of such beneficial interactions have been made in forestry (Padilla & Pugnaire, 2006) and agriculture (Li et al., 2014). A number of studies have shown that plant–plant facilitation can lead to increased productivity and increased yields in natural and agricultural systems (Brooker et al., 2016; Li et al., 2014; Wang et al., 2019).

Besides maximizing yield, the quality or composition of crops has been less often studied but is of crucial concern in terms of nutritional value of the crop to the farmer and to the consumer (Halford et al., 2015). Various factors reportedly influence crop composition and quality directly or indirectly (Popa et al., 2019). A comparison between conventional and organic management in strawberries revealed a higher nutritional value in organic strawberries with higher levels of anthocyanins, ascorbic acids and more intense sensory colour characteristics (Crecente-Campo et al., 2012). Other studies showed that the cultivation of green manure precedent to the crops can alter the composition of organoleptic properties of eggplants (Radicetti et al., 2016), as well as increase the vitamin C content and affect other compounds in okra (Adekiya et al., 2019) and tomatoes (Agbede et al., 2019). Moreover, unfavourable environmental conditions such as salt, drought, freezing, hypoxia, osmotic stresses or early senescence may induce biochemical compensation processes where primary plant metabolites, such as carbohydrates, are interconverted to cope with stresses (Halford et al., 2011). Stresses or specific nutrient availability or absence can also induce an altered gene expression for certain enzymes, which may be associated with secondary metabolite synthesis (Halford et al., 2011). Soil microbiota can influence growth, phenology and seed production of plants (Rodríguez-Echeverría et al., 2013). Vice versa plant diversity and community composition shape microbial soil communities (Rodríguez-Echeverría et al., 2013). Soil microbes can mediate plant traits such as leaf size, frost sensitivity, seed mass as well as the architecture, size and distribution of roots and their nutrient uptake, thereby having a significant influence on plant performance (Friesen et al., 2011). Thus, it is probable that there is as well an influence on crop biochemical states and processes which might alter crop quality.

In many agricultural systems, the primary interest is not in maximizing the overall productivity of the system but rather optimizing the growth conditions for one crop plant species. In agricultural fields, non-crop vegetation can occur unintentionally as weeds or spontaneous vegetation or intentionally as sown cover crops. Non-crop vegetation, intentional or unintentional, is often perceived as competing with crops for nutrients and water (Belmonte et al., 2018) and is typically removed (Ryan et al., 2009). Agricultural weed management practices such as tillage or herbicide application can substantially alter plant and animal communities and interspecific dynamics, thereby disrupting ecological interactions (Banerjee et al., 2019). In contrast, low-intensity management has been shown to facilitate higher levels of biodiversity in agricultural systems and increases connectivity between organisms of different functional guilds and trophic levels (Banerjee et al., 2019; Hartman et al., 2018; Hole et al., 2005; Marshall et al., 2003), thereby potentially facilitating beneficial interactions for crop performance (Vukicevich et al., 2016). An increased plant biodiversity can, thus, be either detrimental, by competition, or beneficial, by facilitation, for crop performance. It is however currently unclear if and how the presence of spontaneous plants influences the composition (quality) of crops. Whether plant species are beneficial or detrimental for other plants is determined by their function in the system (Loreau et al., 2001). This can lead to beneficial species interactions between certain functional groups of plants known as facilitation. For instance, legumes are known for contributing to an important function by establishing a symbiosis by building root nodules that contain nitrogen-fixing bacteria, Rhizobia (do Vale Barreto Figueiredo et al., 2013). These N-fixing plants can increase the soil N resource pool and increase crop yield (Fustec et al., 2009) and change crop composition (Ovalle et al., 2010).

A central point in fruit production is often the limited production capacities of the crop plant which results in a trade-off between fruit quantity and quality (Bravdo et al., 1984; Link, 2000). In vineyards, the improvement of berry quality is more important than maximizing yield. As common viticultural management practice, farmers deliberately reduce the number of grape clusters per plant to enhance the quality of the remaining grapes (Poni et al., 2018). Vineyards therefore present an excellent system to investigate potential beneficial effects of biodiversity on crop quality rather than quantity. Grape quality is not determined by one single, isolated indicator, but rather by a suite of quality parameters that influence wine fermentation and final quality (Poni et al., 2018). The assessment of grape berry maturity requires timely information to determine the optimal point of harvest (Dambergs et al., 2015). The content of sugar, malic and tartaric acids and yeast assimilable nitrogen (YAN) are some of the most critical quality parameters (Bell & Henschke, 2005; Dambergs et al., 2015). Optimal ranges for the composition of quality parameters depend on grape variety and farmers' preferences (Conde et al., 2007). Over the course of berry maturation, sugar levels increase while acidity decreases. Physiological ripeness is reached when the sugar content in grape must is sufficiently high for the desired alcohol content in the wine without reducing acidity too much (Conde et al., 2007). Tartaric acid is generally more desired than malic acid (Conde et al., 2007). The nitrogen content in must is crucial for the fermentation activity of the yeast and to assure appropriate fermentation, YAN concentrations should be >140 (mg/L) (Bell & Henschke, 2005).

Research projects evaluating effects of agricultural management practices often solely consider the net effects of the treatment on crop performance such as yield or growth (Ryan et al., 2009), without considering potential beneficial interactions of the crop with other plants. To reveal biodiversity-mediated effects and to disentangle direct and indirect effects of management requires the evaluation of system-level hypotheses which are based on ecological interaction principles. The aim of our study was to investigate how grape quality parameters respond to management practices (vegetation removal) and whether spontaneous vegetation might have beneficial effects. We first compared the multivariate response of grape quality parameters across two varieties (*Pinot noir* and *Chasselas*). We used structural equation modelling to evaluate the responses of grape quality parameters to a gradient of management intensity and spontaneous vegetation community characteristics based on three non-exclusive hypotheses of competition, complementarity and facilitation. We expect that management intensity will be the most important predictor for grape quality parameters if competition is the dominating interaction between spontaneous and grape plants. However, if complementarity or facilitation mechanisms are most relevant for grape quality, then plant species richness or the abundance of N-fixing plants will be important predictors. Distinguishing between the two latter factors will give information about the generality or specificity, respectively, of complementarity effects. Evaluating and understanding these interactions and integrating beneficial mechanisms into practice might help achieving more sustainable and ecological agricultural systems (Doré et al., 2011).

2 | MATERIALS AND METHODS

2.1 | Study sites and treatment

We studied 33 vineyards spread across a distance of about 38 km within a mosaic-like viticultural landscape in the Canton of Valais, in southern Switzerland. Vineyards were managed under conventional management with inputs of agrochemical products according to vine-growers' customs (additional information see Appendix 1a, Table S1). The region is characterized by low annual precipitation rates of about 600 mm (Canton Du Valais, 2017). The size of the vineyards ranged from 302 to 10,000 m^2. Two different wine varieties were included *Chasselas* (n = 15 sites) and *Pinot noir* (n = 18), evenly spread across weed removal treatments. Spontaneous vegetation in vineyards was removed by herbicide application or tillage in every inter-row (n = 10 sites), or every-second-inter-row (n = 13 sites), or vegetation was not removed but cut 2–4 times per season (n = 10 sites). In each study year (2015–2017), we determined total soil N content with the Dumas combustion method (Elementar Analysensysteme GmbH, Langenselbold, Germany) from a mixed soil sample (10 linear subsamples per site at a distance of about 3–5 m) collected from the 3rd and 4th inter-row, starting from the south east corner, of each vineyard (Appendix 1b). We also determined pH, C/N ratio and soil organic matter (SOM) from the same soil samples. Although vineyards varied in many environmental and soil conditions that might influence grape quality parameters, there was no bias in environmental parameters with regard to the vegetation management intensity (Appendix 1a, Table S2).

2.2 | Plant survey

Plant surveys were conducted in 2015 and 2016 in spring (April/May) and autumn (October/September), but only one survey was conducted in 2017 (June). We determined total vegetation cover (%), plant species richness and cover of each species (%) in 1 m^2 plots (total number of plots = 330), in the inter-row space (between two rows of grapevine plants), in two adjacent rows in each vineyard, the same rows that were used for soil analyses (above) and grape sampling (as described below; Appendix 1b). Vegetation plots were placed in each 3rd and 4th inter-row from the south east corner of each vineyard 10 and 15 m from the margin of the plot to avoid edge effects. The spontaneous vegetation across vineyards was rather heterogeneous. However, in each vineyard, vegetation was sampled five times along the grapevine rows, thus was expected to capture this spatiotemporal heterogeneity between vineyards. The vegetation data were averaged within each vineyard.

Linear mixed-effect models were built to test the effect of management intensity on plant species richness and cover of N-fixing plants, where 'vineyard' was used as random factor and the cover of N-fixing plants was transformed as 'log($x + 1$)'.

2.3 | Grape collection and FTIR analysis

In each year, we collected berries for grape juice analysis. We collected 200 berries per site, one each from arbitrarily chosen 200 grape clusters from two rows of each vineyard, taken alternately from the top, the middle and the lower tip of a grape cluster (Appendix 1b). The berries were collected directly adjacent to the rows where soil samples and vegetation survey was performed (Appendix 1b). The spatial range and number of individual grapevine plants from which the berries were taken differed as our study sites covered a large variation of vineyard sizes (see above section 'study sites & treatments' and Appendix 1a and b). The collection date was chosen to be as close as possible to the farmers' grape harvest and was approximately 2 weeks earlier for *Pinot noir* than for *Chasselas*. In each year, all berries from one vineyard were pooled and mashed and the juice was collected for subsequent Fourier-transform infrared spectroscopy (FTIR; Patz et al., 1999) to determine YAN (mg N/L), grape sugar content (°Oechsle), malic acid (g/L), tartaric acid (g/L) as well as total acidity and pH. FTIR analysis was performed at the Swiss Agricultural Research Institute Agroscope, Changins (CH).

2.4 | Statistics—SEM

Variables were standardized to comparable scales prior to analysis (Grace et al., 2010); grape sugar content (°Oechsle) was divided by 10 and YAN (mg N/L) by 100. Prior to structural equation modelling (SEM) analyses, a meta-model was developed to specify in general terms the primary questions of interest and the suite of specific SEMs to be considered (Grace et al., 2010). As shown in Figure 1, the overall question of interest in these analyses was whether grape quality parameters depend on management intensity and if so, whether spontaneous plants or variations in soil N content might have additional effects. Table 1 complements Figure 1 by providing a description of the measurements associated with each concept and the rationale related to scientific interpretations.

Implied by the meta-model (Figure 1) is a set of specific SEMs that can be used to address the primary questions of interest. In the development of specific models, we constrained our examinations to avoid models too complex to support given the available number of samples ($n = 33$ vineyards; Grace et al., 2012). In this case, several steps (outlined below) were taken to minimize model complexity while retaining essential components. It was also decided, based on preliminary analyses, to average the values obtained at a site over the 3 years of data collection to reduce measurement error and natural variation (Regan et al., 2002).

As a first stage in the SEM process, grape quality parameters were modelled as multiple indicators of a general multivariate response (Figure 2; Appendix 1c). Prior to modelling, we screened possible indicator variables for inclusion. It was observed that total acidity was almost perfectly explained by the sum of tartaric and malic acid concentrations; thus, total acidity was excluded as a unique measure. Because of the role that YAN content plays in the assessment of grape quality parameters, this measure was used as the fixed indicator in the specification of a four-indicator latent-variable model. The two grape varieties were modelled simultaneously using multi-group procedures (Grace, 2006, Appendix 1c). The hypothesis of equal indicator loadings across varieties was evaluated to determine whether the two varieties reflect a common set of trade-offs among quality parameters.

The second stage in the SEM analysis involved comparing three complete models representing key contrasting hypotheses of interest (Figure 2). The first model, the Net Effect Model, was developed to represent the influence of management intensity on grape quality parameters through the control of spontaneous vegetation. Separate analyses confirmed a clear and linear relationship

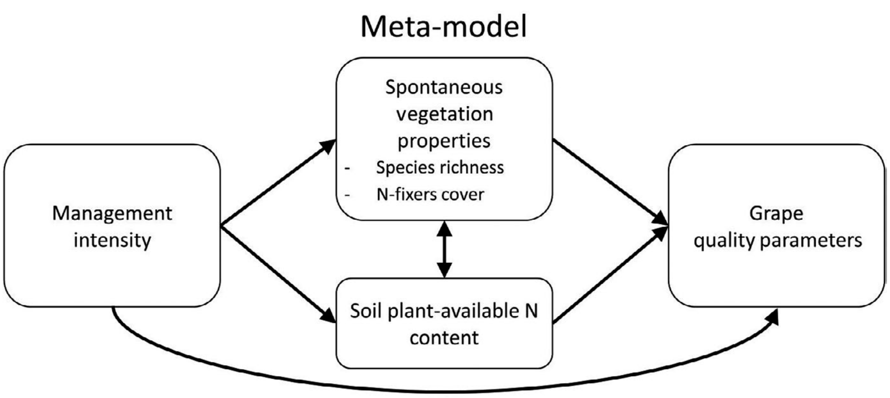


FIGURE 1 Meta-model representing general hypotheses to be considered using structural equation modelling

TABLE 1 Concepts related to the structural equation meta-model (Figure 1) and their relationships to measured variables

Variable of interest	Measurements	Scientific rationale
Management intensity	Intensity is a three-level index {1,2,3}. 1 = minimal control of inter-row vegetation, 2 = vegetation removal in every other row between grape plants, 3 = vegetation removal in all rows between grape plants	The primary purpose of management is to reduce competitive effects of spontaneous plants on grape plants. It is assumed that competition primarily acts through reductions in soil water and nutrients, but other forms of interference could be possible
Spontaneous vegetation properties	Plant species richness (numbers), abundance of N-fixing plants (% cover),	One possibility we wished to consider was a general beneficial effect of plant richness on grape quality parameters due to complementarity Another possibility of interest was a specific effect of the abundance of N-fixing plants on grape properties due to facilitation
Soil nitrogen	Total soil N content (%)	We considered it possible that variations in total soil N might help explain variations in grape YAN. Such an effect either might or might not be indirectly related to management intensity
Grape quality parameters	YAN concentration Sugar concentration Tartaric acid Malic acid Total acidity pH	We measured a suite of standard grape chemical parameters of importance for wine making. While all of these parameters determine the character of wine, YAN concentration is perhaps of primary concern because of its critical role in the fermentation process (Bell & Henschke, 2005)

between management intensity and the total cover of spontaneous vegetation, supporting our interpretation of this model. The second model examined (the Biodiversity Model) included the possibility of an additional mediating mechanism, whereby low-intensity management would result in elevated spontaneous plant species richness, which, in turn, may affect grape quality parameters. A third model (the Functional Diversity Model) considered the mechanism of low management intensity on elevated abundance of N-fixing spontaneous plants, which, in turn, might influence grape quality parameters. Not shown in Figure 2 is a fourth model that examined whether variations among sites in soil nitrogen, when added to the model, might explain additional variation in grape quality parameters.

All analyses were performed using R (R Core Team, 2019). SEM analyses were performed using the LAVAAN package (Rosseel, 2012). Details of model development and evaluation are described in Appendix 1c Model comparisons were based on a modern 'weight of evidence' approach that combines the use of *p* values and information criteria in model selection (Grace, 2020).

3 | RESULTS

3.1 | Plant survey

We found 170 different plant species across all vineyards and years. Approximately 49% of total plant species counts consisted of the top 16 most frequently found species (Figure 3).

The family of F*abaceae* was represented by 17 species, which composed together about 17.2% of all species counts. These were *Trifolium repens*, *Trifolium campestre*, *Vicia sativa*, *Medicago lupulina*, *Vicia sepium*, *Trifolium pratense*, *Vicia cracca*, *Vicia lathyroides*, *Lotus corniculatus*, *Vicia dumetorum*, *Medicago minima*, *Ononis pusilla*, *Ononis rotundifolia*, *Anthyllis vulneraria*, *Lathyrus pratensis*, *Vicia onobrychioides* and *Vicia sp*. As expected, plant species richness (estimate: −2.6, $p < 0.001$) and cover of N-fixing plants (estimate: −0.57, $p < 0.001$) decreased with increasing management intensity. On average, the number of spontaneous plant species ranged in *Chasselas vineyards* in low-intensity management between 6.1 and 9.5, in intermediate intensity management between 3.4 and 6.3 and in high-intensity management between 0.9 and 4.7 across all years. In vineyards of *Pinot noir*, the average number of plant species in low management ranged from 5.7 to 11.7, in intermediate management between 5.7 and 7.9, and in vineyards with high management intensity between 1.8 and 5.3 species. On average, the cover of N-fixing plants in *Chasselas* vineyards ranged for low, intermediate and high management intensity between 0%–16.1%, 0%–4.3% and 0%–0.2%. In Pinot noir, the cover of N-fixing plants ranged between 0.3%–8.4%, 0.04%–6.6% and 0%–0.4% in low-, intermediate- and high-intensity management, respectively.

3.2 | Apparent effects of management on grape quality parameters

The net (aka 'marginal') relationships of grape quality parameters to management intensity are presented in Figure 4. The variety *Chasselas* showed a higher YAN and a lower sugar content at higher management intensities. In contrast, grape quality parameters for *Pinot noir* showed no obvious relation to management intensity.

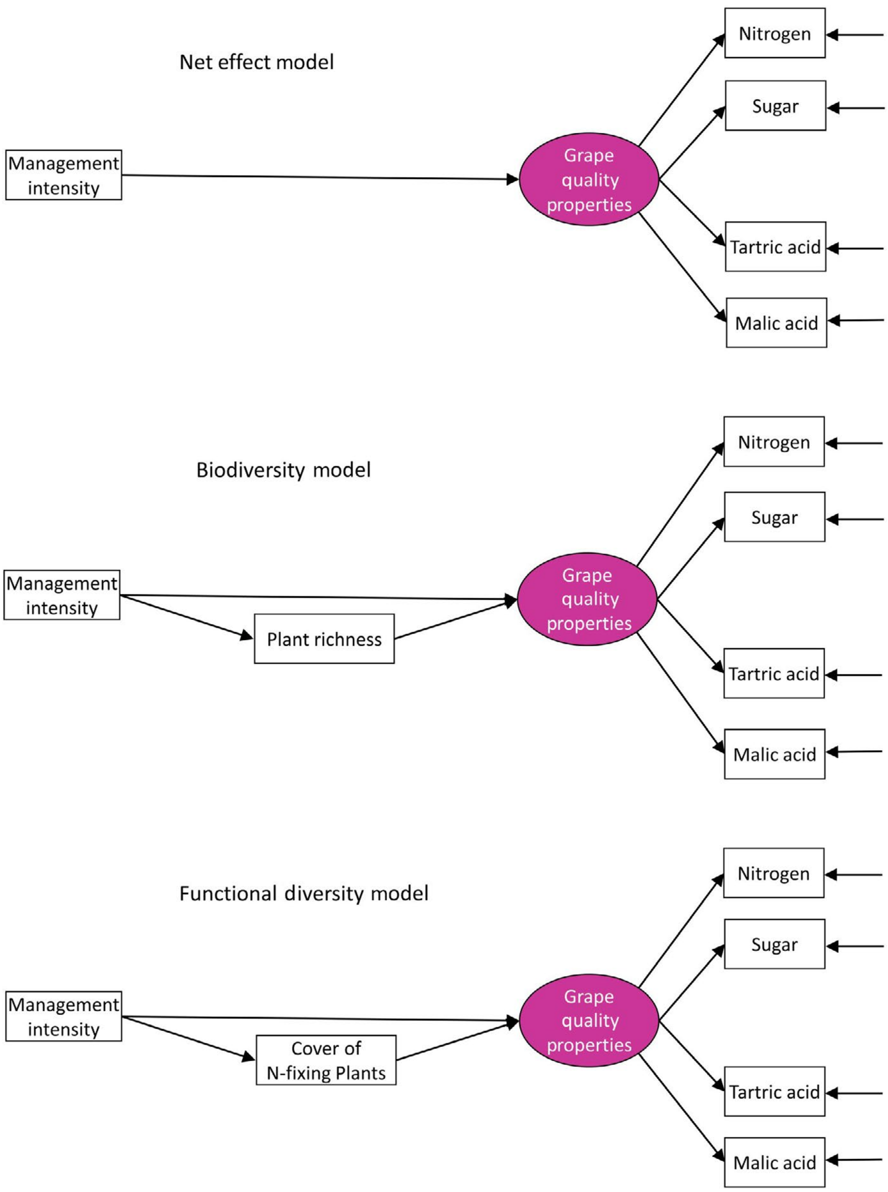


FIGURE 2 Three competing structural equation models (SE models) evaluated in the study. The Net Effect model represents the hypothesis that grape quality parameters vary as a function of management intensity in relation to the degree to which management reduces competitive effects of spontaneous plants on grape plants. The Biodiversity model includes plant richness and represents general complementarity interactions. The Functional Diversity Model includes the abundance of N-fixing plants and tests, in contrast to the Biodiversity model, a facilitation interaction between spontaneous N-fixing and grape plants

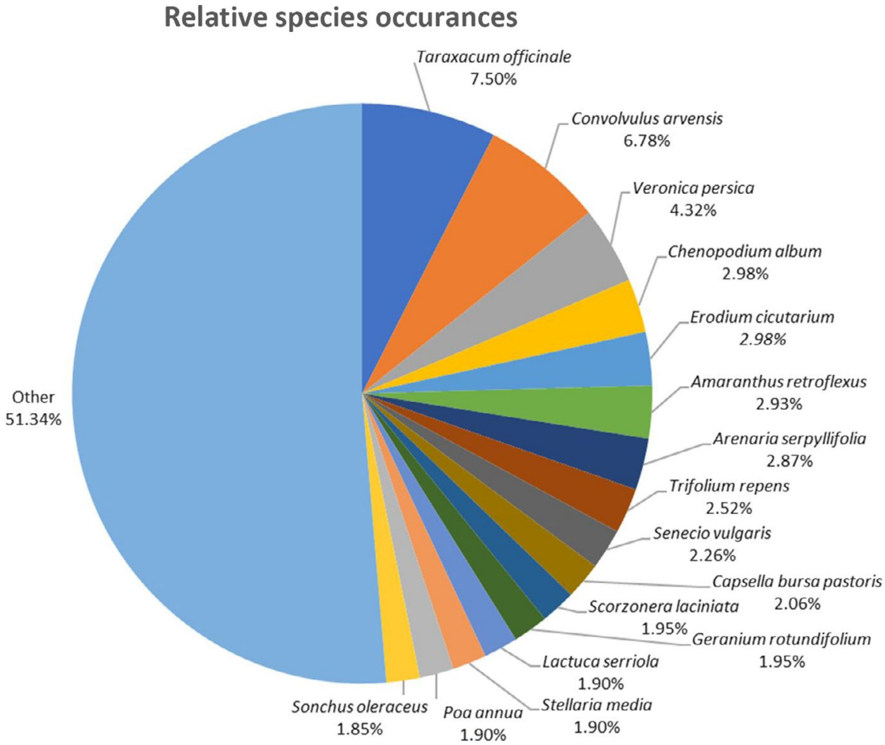
Our evaluation of complete SEMs (Figure 2) began with the Net Effect Model. Initial assessment showed the need to include an additional link from Management Intensity to Tartaric Acid in all the models. Fit statistics for the Net Effect, Biodiversity and Functional Diversity Models, as well as a model that included soil nitrogen, are given in Table 2.

3.3 | Structural equation modelling results

The Net effect model revealed a significant contribution of management intensity on grape quality parameters judged by the model fit statistics (Grace, 2020, Appendix 1c, Boxes 9–11B and Table 2). In viewing the results in Table 2, the reader should keep in mind that low p values associated with chi-square test statistics indicate poor model fit. Furthermore, including plant richness as a predictor variable (Biodiversity model) showed no significant contribution to explaining grape quality parameters for either variety (Appendix 1c, Box 14). The Functional Diversity Model, which included the abundance of N-fixing plants, showed a significant contribution to explained variation of grape quality parameters (Appendix 1c, Boxes 24–25), which markedly increased the explained variation in the variety *Pinot noir* (Table 2). Thus, the comparison of model fit statistics (Table 2) supported the Functional Diversity Model. Moreover, adding soil nitrogen to the best-fitting model (Functional Diversity Model) did not lead to an improvement in model fit as judged by the test statistic and low p value (Table 2). Therefore, the Functional Diversity Model was chosen as the best model for further interpretation of paths.

The two grape varieties reacted similarly to management intensity but differently to mediated effects. Increased management intensity directly affected grape quality parameters of both varieties (Figure 5). For *Chasselas*, the abundance of N-fixing plants as mediator showed no significant effect on grape quality

FIGURE 3 Relative plant species occurrences of total counts of plant species across all vineyards and years. The top 16 most frequently found plant species are labelled with Latin species names. The label 'Other' consists of 154 other spontaneous plant species with occurrences of <1.85%



parameters (Figure 5), while for *Pinot noir* a strong positive effect was observed (Figure 5). Management intensity negatively affected the abundance of N-fixing plants in the vineyards of both varieties (Figure 5).

Yeast assimilable nitrogen was most strongly associated with grape quality parameters after management intensity was included in the model in both grape varieties, recognizable by comparing latent variable loadings (Appendix 1c, Appendix 2 R code). This effect was stronger in *Chasselas* than in *Pinot noir*. Management intensity also had a relatively strong, direct, negative effect on tartaric acid in *Chasselas*, which was almost eliminated by a positive indirect effect via the latent variable.

The total effect of management on grape quality parameters consists of the sum of direct and indirect, plant-mediated effects (Table 3). For *Chasselas*, the indirect effect is not significant; thus, only the direct effect is relevant while for *Pinot noir*, both pathways are relevant for the total effect of management.

4 | DISCUSSION

In both varieties, grape quality parameters, as latent multivariate response variable, revealed a consistent, integrated trade-off between nitrogen content and acids on the one hand and sugar on the other. Grape quality is determined by many chemical parameters. In general, it is often an optimal composition of these parameters while the optimum is a range which varies for each grape variety and year. In practice, the moment of harvest is often determined when the sugar content reaches the lower limit. For high-quality wines in 2019, the lower threshold for sugar content in Chasselas was 77.6 °Oechsle and for Pinot noir 91.9 °Oechsle (Memo_Natürlicher Mindestzuckergehalt in 2019. Weinbauamt Kanton Wallis, 2019). There are no such limits published for the different acids. Management intensity influenced grape quality parameters with a strong regulatory effect on grape nitrogen. Yeast assimilable nitrogen is one of the most critical parameters in wine making and has to be above a critical threshold of 140 mg N/L for proper fermentation (Bell & Henschke, 2005). Grape juices with values falling below this threshold could lead to a premature halt in the fermentation process, which has negative consequences for the wine quality and consequently economic loss (Bell & Henschke, 2005). The historical removal of spontaneous vegetation appears therefore intuitive, at a first glance, from an agriculturist's perspective to maintain good quality of grapes.

Both grape varieties profited from the reduced competition between the vine and the spontaneous vegetation. While competition was the most relevant interaction determining grape quality parameters in *Chasselas*, the mediation via spontaneous plants appeared to be crucial for grape quality parameters in *Pinot noir*. The positive response of *Pinot noir* towards the abundance of N-fixing plants was similar in magnitude to the positive effect of management intensity (Table 3). However, management intensity also reduced the abundance of N-fixing plants and impeded the positive vegetation-mediated effect. In *Pinot noir*, the opposing direct (competition) and indirect (N-fixing plants mediated) effects of management were offsetting each other, resulting in a lower total effect of management on grape quality, which explains the apparent lack of a management effect on *Pinot noir* grape quality parameters in a simple bivariate analysis (Figure 4).

Structural equation modelling revealed that both management and spontaneous vegetation affect grape quality parameters of *Pinot noir* but the opposing direct and indirect pathways are offsetting

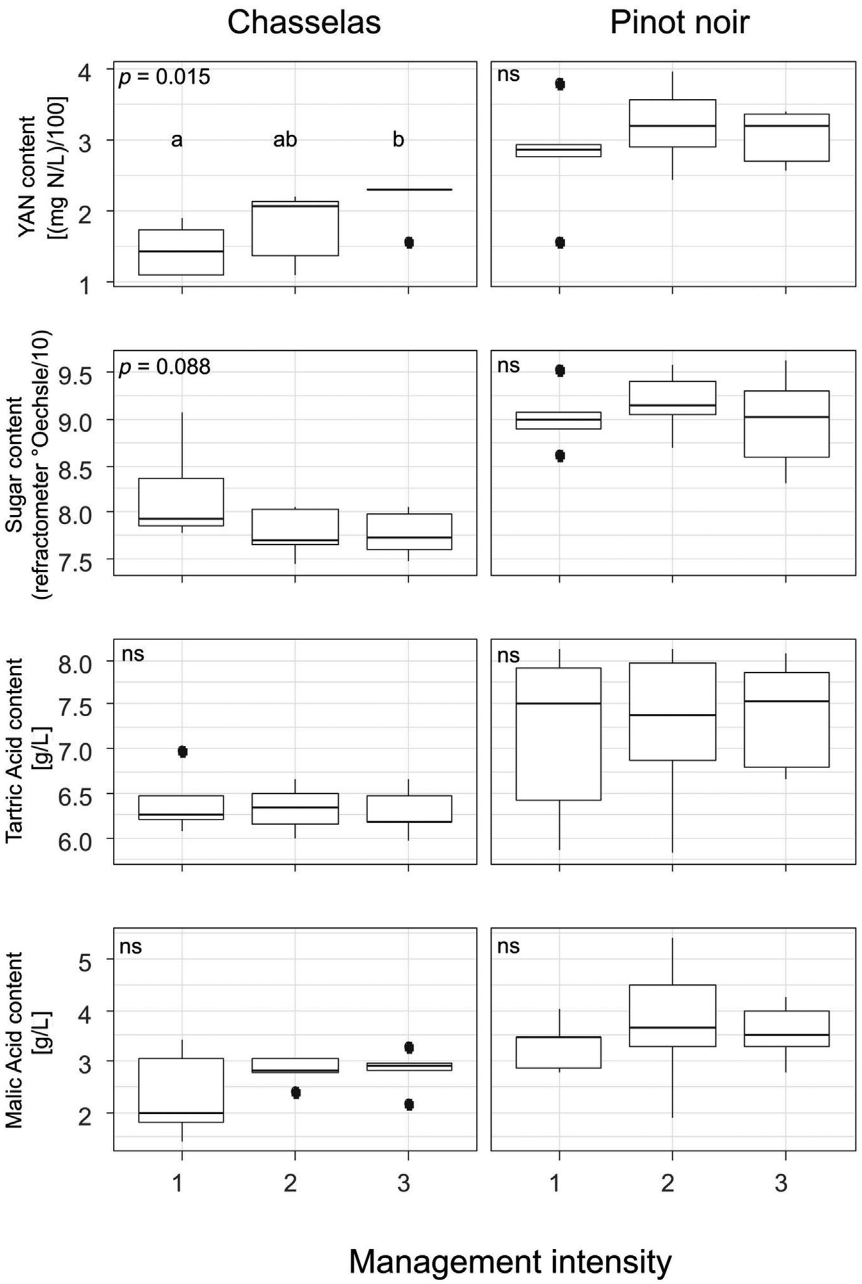


FIGURE 4 Boxplots illustrate relationships of management intensity (1 = low, 2 = intermediate, 3 = high) on grape juice quality parameters nitrogen (YAN), sugar (refractometer °Oechsle), taratric acid and malic acid. p values were obtained from linear regression ($N = 33$). Significant differences between groups (a, ab, b) were obtained by post-hoc pairwise comparisons

each other and therefore do not appear in the bivariate analysis. Our analysis underlines the benefit of using a latent response variable to illustrate a response of a composition of parameters of interest, which is not possible in bivariate analysis, and the usefulness of SEM to reveal hidden offsetting effects. Not revealing the hidden offsetting effect of management and N-fixing plants leads to different conclusions, which would be the apparent insensitivity of *Pinot noir* to management intensity and could result in counterproductive management recommendations.

The positive influence of N-fixing plants on crop plant nutrition is a well-known, frequently observed effect in agroecological studies and commonly related to N enrichment of the soil (Fustec et al., 2009). However, including soil N content did not significantly better explain grape quality parameters than the original Functional Diversity Model. This indicates that the observed effect may not derive from an enriched soil N pool directly, but that interspecific plant–plant (or plant–microbe) interactions are involved. It has been shown by stable isotope labelling that non-crop vegetation can actively exchange nutrients with grapevine plants via arbuscular mycorrhiza hyphal networks (Cheng & Baumgartner, 2004; Johansen & Jensen, 1996). However, the relative importance of facilitation compared to competitive interactions differs among grape varieties within the same crop species, indicating a high specificity. Generally, interactions with specific mycorrhiza can be beneficial only under certain soil conditions, or for one crop species but not for another (Berg & Smalla, 2009). Lack of understanding these specificities might explain mixed success of attempts to use commercially available, standardized microbial inoculates to stimulate facilitation in arable crops as reviewed by Owen et al. (2015), who revealed a lack of consistent proof of the effectiveness of such inoculants.

TABLE 2 Fit statistics for models examined

Model	Variables	Model fit parameters: Test statistic χ^2	df	p value (chi-square)	AIC	Grape quality parameters R^2 (average): Chasselas	Pinot noir
Net effect	Management intensity	15.096	12	0.178	371.462	0.50	0.04
Null model	Management intensity == 0	27.356	15	0.026	377.637	0.25	0.18
Biodiversity model	Management + Plant richness	18.675	18	0.412	435.71	0.51	0.09
Null model	Plant richness == 0	20.529	20	0.425	433.261	0.49	0.02
Functional diversity model	Management + N-fixers	23.733	18	0.164	462.354	0.50	0.28
Functional diversity model (modified)	Chasselas N-fixers == 0	25.000	19	0.161	461.408	0.45	0.27
Null model	N-fixers == 0	27.699	20	0.117	461.968	0.49	0.02
Soil N	Management + Soil N	29.223	18	0.046	475.045	0.496	0.038
Null model	Soil N == 0	31.638	22	0.084	469.339	0.493	0.019

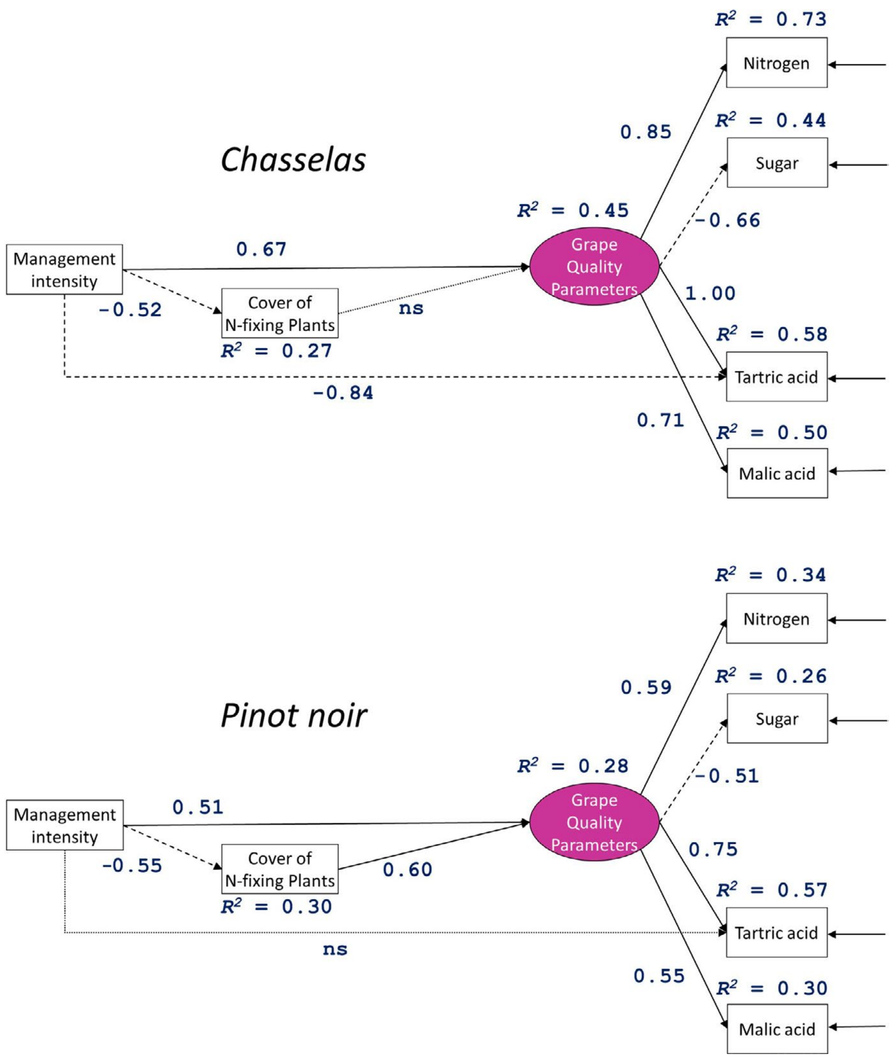


FIGURE 5 Structural equation model for *Chasselas* (above) and *Pinot noir* (below) including management intensity and cover of N-fixing plants as well as a multi-response latent variable (in ellipse) representing grape quality parameters. Measured variables are illustrated in rectangles. All included relationships are supported by the data for at least one of the varieties, dotted lines are deemed to be not supported (ns) for this variety, solid lines are positive effects and dashed lines are negative effects. Standardized path coefficients are shown on the graphs. Grape quality parameters in *Chasselas* strongly vary with variations in management intensity and more specifically, grape juice nitrogen (YAN) is higher where there is greater management intensity. Grape quality parameters in *Pinot noir* are associated with management intensity but also with the cover of N-fixing plants. More precisely, the cover of N-fixing plants predicts increased YAN in the grape juice

TABLE 3 Standardized direct and indirect effects of management on grape quality parameters, from Figure 5, for both grape varieties. For '---', effects could not be calculated as the best model did not include this path

Effect	Description	*Chasselas*	*Pinot noir*
Direct effect	Management intensity effect on grape quality parameters	0.67	0.51
Plant-mediated pathways	Management effect on N-fixing plant abundance	−0.52	−0.55
	N-fixing plants' effect on grape quality parameters	---	0.60
Indirect effect		---	−0.33
Total effect		0.67	0.18

In grapes, environmental factors such as light, temperature, water and nutritional status can mediate metabolic processes, for example, flavonoid biosynthesis (Downey et al., 2006; Halford et al., 2015). Our results indicate that co-occurring plant species may affect individual grape varieties differently, potentially via similar mechanisms as other environmental factors. Soil nutrients can determine the expression of genes involved in the synthesis of enzymes leading to altered composition of secondary plant compounds in crops (Downey et al., 2006; Halford et al., 2015). The suggested genetic control of these mechanisms might have contributed to the contrasting effects in different varieties of the same crop species (Postles et al., 2013).

These findings imply that, similar to other management practices such as irrigation or canopy trimming, also the maintenance and composition of inter-row non-crop vegetation should be tailored to the needs of the individual cultivar (Downey et al., 2006). Using non-variety-specific seed mixtures that are recommended as cover crops in vineyards, farmers may unintentionally increase competition rather than promote beneficial interactions (Miglécz et al., 2015). This illustrates the necessity for thorough testing and validation of such relationships in different agricultural systems, between different crops and non-crop vegetation, and to identify possible microbial mediators (Duchene et al., 2017).

While overall productivity of a system can be improved by generally increasing biodiversity, this may not result in increased crop yield or quality in agricultural systems and could even increase competition between the crop and the non-crop vegetation (Tilman et al., 1997). The specificity of plant–plant or plant–microbe interactions and nutrient-dependent gene expression of different varieties are very promising concepts for ecological intensification of agricultural systems, where beneficial interactions are utilized for the purpose of improving agricultural output (Doré et al., 2011). However, the inconsistent effectiveness of microbial inoculants or contrasting responses of different crop varieties stresses the need for a precision agriculture approach, where deficiencies of crops should be targeted at the field/cultivar/farm level rather than following general recommendations (Berg & Smalla, 2009; Downey et al., 2006; Gebbers & Adamchuk, 2010; Owen et al., 2015).

Even though there was a positive effect of N-fixing plant abundance on grape quality parameters, it is likely that there is a trade-off at high densities of N-fixers, due to competition for other resources (e.g. water or nutrients) with the crop. It is important to determine the optimal densities of functional group abundance and therefore facilitate a more targeted implementation of beneficial ecological interactions. Considering the combination of niche theory and facilitation effects of increased biodiversity, a diversified N-fixer community could potentially amplify the beneficial interactions (Fargione et al., 2007).

Our study is an explorative study under realistic conditions in a locally representative viticultural landscape with a high degree of environmental variation. We cannot exclude that other factors concerning viticultural management practices such as irrigation, grapevine planting distance, pruning systems or environmental factors such as slope exposure, soil parameters or their interactions may have affected grape quality properties additionally, but we have no indication that environmental variation was biased with regard to vegetation treatments (Appendix 1a). Due to limitations of statistical power, however, we could not include more factors in the SEM.

5 | CONCLUSIONS

We revealed a hidden offsetting effect where increased management intensity negatively affected the cover of a group of plants with a specific function, which had a positive effect on grape quality. These opposing effects were only revealed by SEMs and would have been overlooked in conventional analyses. Whether spontaneous vegetation turns out to be beneficial or detrimental to the crop may depend on the individual cultivar. This is critical for management recommendations as wine makers unknowingly would work counteractively to their interests by removing all spontaneous vegetation or by maintaining non-specific plant communities. Great potential for the sustainable improvement of crop quality lies in the careful selection and balancing of companionship by non-crop plant species and cultivars. While this study was carried out in vineyards, the relationships revealed here might be relevant in other perennial cropping systems as well. However, these combinations and the potential trade-off at high densities require thorough testing.

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AUTHORS' CONTRIBUTIONS

M.S. and S.B. designed the project; M.S. performed the data collection; M.S. and J.B.G. analysed the data with some input by S.B. All authors significantly contributed to the development of this manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.z8w9ghx83 (Steiner et al., 2021).

ORCID

Magdalena Steiner https://orcid.org/0000-0002-5568-6607
James B. Grace https://orcid.org/0000-0001-6374-4726
Sven Bacher https://orcid.org/0000-0001-5147-7165

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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