

## LETTER

# Identifying mechanisms that structure ecological communities by snapping model parameters to empirically observed tradeoffs

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### Abstract

Theory predicts that interspecific tradeoffs are primary determinants of coexistence and community composition. Using information from empirically observed tradeoffs to augment the parametrisation of mechanism-based models should therefore improve model predictions, provided that tradeoffs and mechanisms are chosen correctly. We developed and tested such a model for 35 grassland plant species using monoculture measurements of three species characteristics related to nitrogen uptake and retention, which previous experiments indicate as important at our site. Matching classical theoretical expectations, these characteristics defined a distinct tradeoff surface, and models parameterised with these characteristics closely matched observations from experimental multi-species mixtures. Importantly, predictions improved significantly when we incorporated information from tradeoffs by ‘snapping’ characteristics to the nearest location on the tradeoff surface, suggesting that the tradeoffs and mechanisms we identify are important determinants of local community structure. This ‘snapping’ method could therefore constitute a broadly applicable test for identifying influential tradeoffs and mechanisms.

### Keywords

Cedar Creek, coexistence mechanism, ecological community, grassland ecology, LTER, mechanistic model, predictive model, resource competition, tradeoff.

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## INTRODUCTION

A primary goal of ecology is to understand the mechanisms that determine species coexistence and community composition (Lawton 1999). Almost all known mechanisms that potentially explain observed patterns of diversity assume that species differ in how they interact with one another or with their environments (Chesson 2000; Adler *et al.* 2013; May *et al.* 2016). To enable stable coexistence, these differences must correspond to interspecific tradeoffs (Tilman 1990, 2011; Chesson 2000; Litchman & Klausmeier 2008), such that increased investment by species in strategies that are favoured under some circumstances necessarily require decreased investment in other strategies (see definitions in Box 1) (Stearns 1989; Roff 1992; Zera & Harshman 2001; Roff & Fairbairn 2007). Tradeoffs have therefore been widely suggested as useful indicators for identifying mechanisms that structure ecological communities (Tilman 1990; Kneitel & Chase 2004; Wright *et al.* 2004; McGill *et al.* 2006; Litchman & Klausmeier 2008; Reich 2014).

Ideally, links between empirically observed tradeoffs and hypothesised coexistence mechanisms should be derivable from basic biological assumptions (e.g. Brown *et al.* 2004).

However, it is not clear that such a derivation is possible for many hypothesised mechanisms, which often include ‘high level’ or abstracted characteristics. For example, consider plant dispersal, which can depend on plant height (Thomson *et al.* 2011), seed physiology (Muller-Landau *et al.* 2008), abundances of seed predators (Janzen 1970; Connell 1971), meteorological conditions (Wright *et al.* 2008), or animal vectors (Harrison *et al.* 2013). Although many such selective forces likely guided the evolution of current day plant dispersal strategies, deriving a theory that simultaneously explains mechanistic tradeoffs among these factors seems unfeasible.

A useful alternative strategy has been to relate empirical observations of the relationships among characteristics of species to theoretical tradeoffs among parameters required for coexistence in mechanism-based models (Kneitel & Chase 2004; McGill *et al.* 2006; Litchman & Klausmeier 2008; Adler *et al.* 2013). For example, plant leaf biomass and area can relate to mechanistic parameters in models of light competition (Rüger *et al.* 2012; Farrior *et al.* 2013), and relationships among species foraging rates can be used to derive interaction coefficients in competition models (MacArthur 1970; Chesson 1990). Accurate predictions of species abundances from such

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### Box 1 Working definitions

Community ecology – and in particular applications concerning functional traits and tradeoffs – includes a rich vocabulary of terms, many of which are precisely defined. To avoid confusion, we therefore use the following working definitions in the main text:

#### COEXISTENCE

Stable persistence of multiple species in an ecological community. We follow a classic definition of stability – that is, the ability to recover to an equilibrium state after perturbation (MacArthur 1970; Takeuchi *et al.* 1978; Armstrong & McGehee 1980; Takeuchi 1996). Note that for the model we consider, this is equivalent to the mutual invasibility criterion of Chesson (2000), which is not necessarily true for all multi-species models (Levine *et al.* 2017).

#### COMMUNITY COMPOSITION

The equilibrium abundances of species in a stably coexisting community. Because coexistence implies non-zero species abundances, mechanisms that structure coexistence likewise structure community composition, and vice-versa.

#### MECHANISM OF COEXISTENCE AND/OR COMMUNITY COMPOSITION

A specifically defined rationale explaining observed patterns. Because stable coexistence requires that species differ in how they interact with one another and/or with their environments (Chesson 2000; Adler *et al.* 2013; May *et al.* 2016), we define mechanisms in terms of interspecific differences in strategies that define these species-environment interactions.

#### MECHANISM-BASED MODEL

A model that is intended to mimic the behaviour of a specific set of hypothesised mechanisms (e.g. resource partitioning), in contrast to *phenomenological models* in which parameters are tuned to match predictions to observations without the goal of mimicking hypothesised mechanisms (Evans *et al.* 2016).

#### CHARACTERISTIC

Measurable aspects of an organism or a population of organisms (e.g. monoculture biomass). We use this term rather than *trait* to avoid confusion with existing definitions in functional trait literature (Violle *et al.* 2007).

#### TRADEOFF

Conserved associations or patterns among species characteristics. These can arise either *empirically* from observed patterns, or *theoretically*, based on patterns predicted by a mechanism-based model. Importantly, *interspecific tradeoffs* describe tradeoffs that are shared across multiple species, such that the characteristics of each species could conceivably fall along a single *tradeoff surface*. Such a surface implies that no species can take on strategies that make it a universally superior or inferior competitor under all circumstances, and is therefore a prerequisite for stable coexistence (Tilman 2011).

models have therefore been suggested as evidence that their underlying mechanisms and tradeoffs could be important determinants of local community composition (Kneitel & Chase 2004; Litchman & Klausmeier 2008; Kraft & Ackerly 2014).

However, mechanism-based models are often sensitive to small changes in parameter values, and generally only allow for coexistence in a narrow band of parameter space. Thus, even if models correctly characterise a system's major mechanisms, small amounts of sampling noise or omission of some minor mechanisms could lead to erroneous predictions (Tilman 2011). Consequently, mechanism-based models usually need to be 'tuned' so that predictions better match observations (Pavlick *et al.* 2012; Evans *et al.* 2016; Kunstler *et al.* 2016). But once so tuned, it is unclear whether accurate predictions result from mechanisms in the model, or from fortuitous fitting of an inaccurate model (Adler *et al.* 2013; Kraft & Ackerly 2014). To improve model predictive power without tuning parameter values, a solution proposed by Purves & Pacala (2008) is to assume that species characteristics fall exactly on the 'tradeoff surface' characterised by empirically observed relationships among species

characteristics, and thus to mathematically 'snap' characteristics to the nearest corresponding point on the surface. Unlike methods that tune model parameters until a desired fit is achieved, snapping characteristics to empirical tradeoff surfaces merely smooths across observed relationships among characteristics, based on the assumption that coexisting species must have tradeoffs.

Here, we argue that this method of snapping mechanism-based model parameters to an empirically observed tradeoff surface is not only useful for improving model predictions, but could also constitute a powerful test for identifying the mechanisms responsible for structuring local community composition. We base this claim on the following logic: (1) all coexisting species in a community must be subject to the same tradeoffs, because any species with universally superior strategies would ultimately displace its competitors, and universally inferior competitors would not persist (Tilman 2011); (2) if we correctly identify mechanisms that are responsible for determining coexistence and community composition, and correctly identify important characteristics of species that are related to those mechanisms, we should therefore find conserved

tradeoffs among those characteristics (Kneitel & Chase 2004; McGill *et al.* 2006; Litchman & Klausmeier 2008); (3) if characteristics do not fall perfectly along the tradeoff surface, then parameterising mechanism-based models using characteristics that have been snapped to fall along the surface might reduce sampling noise and help abstract minor omitted mechanisms into the existing model structure, thereby improving predictions (Schaffer 1981; Purves & Pacala 2008); (4) conversely, snapping traits to an incorrect or highly incomplete tradeoff surface should merely obscure their true values and relationships, and thus will not improve predictions. Significant improvements in predictive power should therefore result from incorporating snapped characteristics *if and only if* the modelled mechanisms and tradeoffs correctly correspond to those in the observed system.

We provide a proof of concept for this approach using observations from long-term experiments in a grassland plant community. We first identify ecologically relevant characteristics based on prior observational and experimental studies, and confirm that monoculture measurements of these characteristics fall along an empirical tradeoff surface. We then parameterise a mechanism-based model with either 'raw' observed characteristics, or with characteristics 'snapped' to this surface, and test for changes in the ability of these two model parameterisations to predict species abundances and coexistence in experimentally assembled multi-species communities. Our results show that models with snapped characteristics provide significantly better predictions, consistent with the hypothesis that the mechanisms and tradeoffs we consider are primary determinants of local community structure. This method may therefore be useful for testing hypotheses about coexistence mechanisms, and for making more broadly generalisable species-level predictions in diverse ecological systems.

## MATERIALS AND METHODS

### Site and data collection

To parameterise and test tradeoffs and models, we used data from long-term grassland plant experiments at the Cedar Creek Ecosystem Science Reserve (Cedar Creek) in Minnesota, USA (45.40°N, 93.20°W). Local soils are sandy and strongly nitrogen limited (Tilman 1987). Mean annual precipitation is roughly 77 cm, with average daily summer high and winter low temperatures of 27°C and −14°C respectively.

To parameterise models, we used data from monocultures of 35 grassland plant species grown in seven experiments at Cedar Creek, encompassing 247 plots. Three experiments (experiment numbers E026, E055 and E070) tested effects of soil fertility on competitive hierarchies; three (E120, E123 and E249) tested effects of planted diversity on ecosystem functioning; the last (E111) was a monoculture garden. All plots were hand-weeded annually, and we used data only from 'control' (i.e. unmanipulated) monoculture plots, collected at least 3 years after establishment. To test model predictions, we used observations from 122 multi-species plots from one of the diversity experiments (E120). Plots were 9 × 9 m, seeded in 1994 with randomly chosen mixtures of 2, 4, 8, or 16 species, and weeded annually to remove non-planted species (Tilman *et al.* 1997).

Furthermore details for all experiments are available in Appendix SI. Species names and replicates are summarised in Tables S1 and S2 in the supplement respectively.

### Identifying influential characteristics

We focus on three monoculture species characteristics: above-ground biomass,  $B^*_{\text{mono}}$ , measured as g m<sup>−2</sup> dried live biomass; competitive ability for soil nitrate,  $R^*$ , measured as the per unit mass concentration of nitrate in monoculture soils; and above-ground tissue nitrogen concentration  $q$ , measured as the percent nitrogen in dry leaf mass. Asterisks indicate dynamical variables assumed to be at equilibrium (i.e. no significant time trend – see model derivation below).  $B^*_{\text{mono}}$  was measured with 10 cm-wide clip strips;  $R^*$  was estimated from soil cores taken at 0–20 cm via 0.01M KCl extraction;  $q$  was measured from homogenised subsets of biomass samples. Measurements were taken during 'peak' biomass (late July or early August). Mean values and standard deviations were calculated for each species using mixed-effects regressions to account for differences in sample size among experiments (see Appendix SII).

We use these characteristics because they relate to species abilities to acquire and retain nitrogen, which previous experimental work has shown to be a primary limiting resource at Cedar Creek (Tilman 1987, 1994; Wedin & Tilman 1993; Dybzinski & Tilman 2007). Species that drive soil nitrate to lower concentrations have lower  $R^*$  and are predicted to be superior nitrogen competitors (Wedin & Tilman 1993; Dybzinski & Tilman 2007) (see Appendix SIII for examples). Species with lower  $q$  have higher nitrogen use efficiency because they produce more biomass per unit of aboveground tissue nitrogen (Dybzinski & Tilman 2007). Finally, at fixed  $q$ , higher  $B^*_{\text{mono}}$  indicates that species access and retain a greater proportion of the total available nitrogen in aboveground tissues (Tilman 1994; Dybzinski & Tilman 2007). Note that we do not account for root biomass or its nitrogen content, following the assumption that aboveground tissues are an indicator of annual fluxes, while roots represent longer-term averages of interannual growth, which can be more difficult to model.

To test their potential explanatory power, we fit a series of linear regressions relating these three characteristics, including up to two and three-way interactions, to observed species abundance and total plot biomass in the 122 multi-species plots. Regressions included up to two additional covariates, which were interacted with all other terms in the model: all regressions included percent soil carbon, which is an indicator of nitrogen mineralisation rates (Fornara & Tilman 2008); a subset of regressions included planted species richness, which strongly influences productivity at Cedar Creek (Tilman *et al.* 1997). For all regressions, we log-transformed species abundance, percent soil carbon, planted richness,  $B^*_{\text{mono}}$ , and  $R^*$ , and logit-transformed  $q$  (see Appendix SIV).

### Empirically fitting the tradeoff surface

To test for tradeoffs, we fit a surface to observed  $B^*_{\text{mono}}$ ,  $R^*$ , and  $q$  using ranged major axis regression, which simultaneously minimises errors in all variables. Again, we log-transformed  $B^*_{\text{mono}}$  and  $R^*$ , and logit-transformed  $q$ . This

regression resulted in a two-dimensional plane in transformed parameter space. We then generated tradeoff-based estimates of characteristics by projecting observed values for each species to the nearest location on the fitted tradeoff surface, which we denote as  $\hat{B}_{\text{mono}}^*$ ,  $\hat{R}^*$ , and  $\hat{q}$ . We refer to this process as ‘snapping’ characteristics to the tradeoff surface, in contrast to ‘raw’ characteristic values observed in monocultures. To summarise regression fit, we calculated  $R^2$  using mean squared difference between ‘raw’ and ‘snapped’ characteristic values (n.b. unlike  $R^2$  in Table 1 and Figs 4–5, which result from ranged major axis regression). Detailed methods for the regression and snapping procedures are in Appendix SV in the supplement, and  $R^2$  calculation is described in Appendix SVIII.

### Mechanism-based model

Our mechanism-based model focuses on a tradeoff between species’ competitive abilities and their abilities to access and retain nitrogen, adapted from a previous model suggested for Cedar Creek (Tilman 1994). Species follow a strict competitive hierarchy, in which superior competitors pre-empt nitrogen uptake by inferior competitors, but inferior competitors do not affect superior competitors. Inferior competitors therefore persist only if they can access nitrogen that superior competitors cannot.

Competitive hierarchy in this model is determined by  $R^*$ , such that species  $j$  is competitively superior to species  $i$  if  $R_j^* < R_i^*$ . Annual nitrogen acquisition and retention is represented by species aboveground biomass,  $B_i$ , and nitrogen use efficiency,  $q_i$ . Arranging species from best competitor ( $i = 1$ ) to poorest, dynamics follow:

$$\frac{dB_i}{dt} = c_i B_i \left( 1 - \frac{\sum_{j \leq i} q_j B_j}{S} \right) - m_i B_i \quad (1)$$

where  $c_i$  and  $m_i$  are species per-unit-biomass population growth and mortality rates respectively, and  $S$  is total

available nitrogen. Solving eqn (1) for equilibrium monoculture biomass of species  $i$ ,  $B_{i,\text{mono}}^*$ , yields:

$$B_{i,\text{mono}}^* = \left( 1 - \frac{m_i}{c_i} \right) \frac{S}{q_i} \quad (2)$$

Equation (2) shows that monoculture biomass in this model is determined by the ratio of population mortality and growth rates, which prevents species from obtaining greater than fraction  $1 - m_i/c_i$  of available nitrogen  $S$ .

Substituting eqn (2) into eqn (1) and solving for multi-species equilibrium biomass,  $B_i^*$ , shows that abundance of species  $i$  equals its monoculture abundance, less biomass lost because of nitrogen acquired by superior competitors:

$$B_i^* = B_{i,\text{mono}}^* - \sum_{j < i} \frac{q_j B_j^*}{q_i} \quad (3)$$

Equation (3) demonstrates that in order to persist, poorer competitors must access a greater fraction of total available nitrogen than superior competitors do (i.e. species with higher  $R^*$  must also have higher  $qB_{\text{mono}}^*$ ; Fig. 1e). Equation (3) therefore abstracts a number of potentially complex processes ( $m_i$ ,  $c_i$  and  $S$ ) into a relationship among the three measured monoculture characteristics described above.

### Stable coexistence

Because we assume a strict competitive hierarchy, eqn (3) can be solved sequentially to determine equilibrium abundances for each species in a community, starting with the best competitor (i.e.  $i = 1$ ). Importantly, any equilibrium that is *feasible* (i.e. for which species have non-negative abundances) is also *globally stable* – that is, equilibrium species abundances predicted by this model always correspond to a single, analytically stable equilibrium. We demonstrate this property through linear stability analysis in Appendix SVI.i. A more

**Table 1** Summary of linear regressions fitting species abundance in mixtures as a function of monoculture characteristics

| Model               | Type             | $n$ | $P$ -value | Partial $R^2$ , linear model |       |         |          |          | $R^2_{\text{adj}}$ , major axis regression |               |
|---------------------|------------------|-----|------------|------------------------------|-------|---------|----------|----------|--|---------------|
|                     |                  |     |            | $B_{\text{mono}}^*$          | $q$   | $R^*$   | % Soil C | Richness | Abundance                                  | Total biomass |
| <i>null</i>         | Base model       | 2   | 0.398      |                              |       |         | 1        |          | 0.00                                       | 0.54          |
| <i>null</i>         | Planted richness | 4   | < 0.001    |                              |       |         | < 0.001  | 0.037    | 0.10                                       | 0.46          |
| $B_{\text{mono}}^*$ | Base model       | 4   | < 0.001    | 0.038                        |       |         | < 0.001  |          | 0.10                                       | <b>0.70</b>   |
| $B_{\text{mono}}^*$ | Planted richness | 8   | < 0.001    | 0.038                        |       |         | 0.001    | 0.036    | 0.20                                       | 0.58          |
| $q$                 | Base model       | 4   | 0.01       |                              | 0.005 |         | < 0.001  |          | 0.01                                       | 0.52          |
| $q$                 | Planted richness | 8   | 0.054      |                              | 0.004 |         | 0.001    | 0.036    | 0.10                                       | 0.33          |
| $R^*$               | Base model       | 4   | 0.954      |                              |       | < 0.001 | < 0.001  |          | –0.01                                      | 0.54          |
| $R^*$               | Planted richness | 8   | 0.863      |                              |       | 0.001   | 0.001    | 0.037    | 0.09                                       | 0.48          |
| All traits          | Base model       | 8   | < 0.001    | 0.085                        | 0.001 | 0.017   | 0.001    |          | 0.26                                       | <b>0.70</b>   |
| All traits          | Planted richness | 16  | < 0.001    | 0.081                        | 0.001 | 0.018   | 0.001    | 0.034    | 0.35                                       | 0.53          |
| 2-way interactions  | Base model       | 14  | < 0.001    | 0.08                         | 0.009 | 0.048   | 0.003    |          | <b>0.48</b>                                | <b>0.61</b>   |
| 2-way interactions  | Planted richness | 28  | < 0.001    | 0.092                        | 0.013 | 0.06    | 0.004    | 0.046    | <b>0.63</b>                                | <b>0.64</b>   |
| 3-way interactions  | Base model       | 16  | 0.093      | 0.081                        | 0.01  | 0.049   | 0.004    |          | <b>0.49</b>                                | <b>0.60</b>   |
| 3-way interactions  | Planted richness | 32  | 0.055      | 0.093                        | 0.015 | 0.062   | 0.005    | 0.046    | <b>0.63</b>                                | <b>0.65</b>   |

All regressions include % soil carbon as a covariate. Regressions labelled with ‘planted richness’ also include number of planted species as a covariate. Models labelled  $B_{\text{mono}}^*$ ,  $q$ , or  $R^*$  include only a single characteristic, while others include all characteristics and their interactions. Column ‘ $n$ ’ shows number of parameters in the regression,  $P$ -values show results for ANOVA tests comparing nested models, and partial  $R^2$  describes relative contribution of each term to total explanatory power.  $R^2_{\text{adj}}$  shows model fit from ranged major axis regression comparing observed and estimated values, either for species abundances, or for total community biomass for each planted mixture. Bolded results indicate regressions with  $R^2$  greater than that for the mechanism-based model parameterised with snapped characteristics (though note that except for the most complex regressions, fits are roughly comparable).



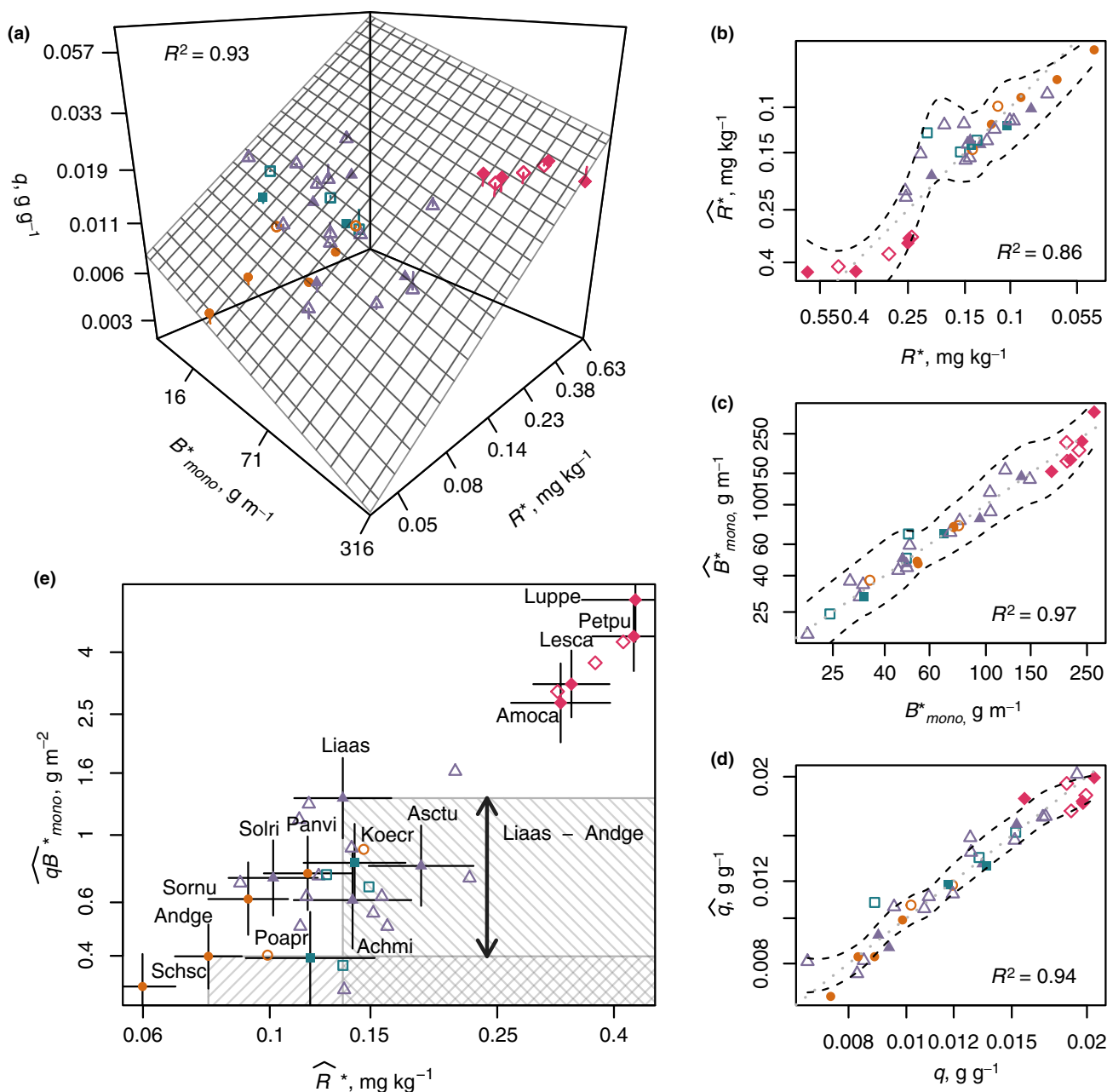
rigorous proof is available in Takeuchi (1996), Theorem 3.3.1, or (more briefly) in Takeuchi *et al.* (1978), Theorem 4.

Because of the strict competitive hierarchy in our model, we can also demonstrate these stable coexistence criteria using pairwise indices of niche overlap ( $\rho$ ) and relative fitness ( $f_2/f_1$ ) *sensu* Chesson (1990). Following Chesson (2000) and Letten *et al.* (2017), pairwise niche overlap and relative fitness in our model are defined as:

$$\rho = [(q_1/q_2)B_{1\text{mono}}^*]^{1/2} \quad (4)$$

$$f_2/f_1 = [(B_{2\text{mono}}^*)^2 / ((q_1/q_2)B_{1\text{mono}}^*)]^{1/2} \quad (5)$$

See Appendix SVI.ii in the Supporting Information for derivation. Defining species 2 as the inferior competitor (with no loss of generality), stable coexistence occurs when  $\rho < f_2/f_1$ .



**Figure 1** Tradeoffs for monoculture aboveground biomass  $B_{\text{mono}}^*$ , competitive hierarchy  $R^*$ , and proportion tissue nitrogen  $q$ . Characteristics snapped to the tradeoff surface are denoted by  $\hat{B}_{\text{mono}}^*$ ,  $\hat{R}^*$ , and  $\hat{q}$ . Points show values for monocultures of 35 species. Green squares show C3 grasses, orange circles C4 grasses, purple triangles non-legume forbs, and pink diamonds legumes. Filled shapes denote species present in multi-species mixtures. (a–d) Raw characteristics fit closely to the tradeoff plane (parameters in Table S3). (e) Species are excluded by competitors that have both lower  $R^*$  and higher  $qB_{\text{mono}}^*$  (species abbreviations described in Table S1). As an example, shaded regions show species excluded by *Andropogon gerardi* (Andge) or *Liatris aspera* (Liaas). Difference in  $qB_{\text{mono}}^*$  between species (e.g. 'Liaas - Andge') shows the amount of nitrogen available to the inferior competitor. Dashed lines and intervals show mean  $\pm$  one standard error for intraspecific characteristic variation.  $R^2$  is calculated from mean squared difference between raw and snapped traits.

Substituting Eqs. (4–5) into this inequality and simplifying yields the criterion for stable coexistence:

$$(q_1/q_2)B_{1\text{mono}}^* < B_{2\text{mono}}^* \quad (6)$$

Because inferior competitors have no effect on superior competitors in our model, we can substitute  $q_1B_{1\text{mono}}^*$  in Eq. (6) with the sum of nitrogen uptake by all superior competitors (i.e. species  $j < i$ ), yielding the stability criteria for multi-species systems:

$$\sum_{j < i} (q_j/q_i)B_j^* < B_{i\text{mono}}^* \quad (7)$$

Note that eqn (7) is identical to the criterion for positive abundance (and thus stable coexistence) in eqn (3).

### Testing predictions

For each of the 122 species mixtures in the experimental multi-species plots, we parameterised two versions of eqn (3): one with raw characteristics, and one with characteristics snapped to the tradeoff surface (n.b. all models also included within-species variability, based on variation observed among replicate monocultures). We compared model outputs to observations from the multi-species mixtures based on predictions of stable coexistence, species-level abundance, and plot-level biomass. Detailed methods for making and testing model predictions are in Appendix SVII and SVIII respectively.

For each multi-species mixture, we used eqn (7) to determine which species were predicted to stably coexist. As a tractable proxy of coexistence in the observed data, we used observations of long-term persistence, including any planted species that appeared in at least one survey since 2001 (i.e. at least 7 years after planting). This accounted for the small spatial scale of the biomass samples, which resulted in rare species being ‘missed’ in some years. This proxy accords well with visual surveys in 2016, which confirmed that almost all planted species persisted in the multi-species plots, though often at low abundance.

For both species abundance and total plot biomass, we quantified mean absolute error (MAE), measured as |observation – prediction|, and report differences as ‘fold change’. Each unit of fold change corresponds to a doubling or a halving – for example, MAE = 1 implies that predictions are either double or half the observed value. For species abundances, we calculated MAE for each plot as the mean error across all species, whereas for total plot-level aboveground biomass, MAE is the difference between observed and predicted productivity. For both plotting and analyses, we replaced predictions or observations of zero biomass with  $0.02 \text{ g m}^{-2}$ , corresponding to the lower 99.9% percentile of non-zero observations.

### Extrapolating from the tradeoff surface

Lastly, we tested whether the tradeoff surface itself could be used to predict average relationships between community productivity and diversity. To conduct these tests, we constructed simulated ‘pools’ of pseudo-species with characteristics for each simulated species determined by randomly choosing a

point on the tradeoff surface. Because characteristic distributions differed between the 35 species grown in monoculture and the subset of those planted in the multi-species plots, sampling was restricted to match the multi-species subset (but not to match the distribution found in individual plots). We then predicted mean aboveground biomass and species abundance distributions for communities of 2–16 species drawn from these simulated species pools, and compared predictions to mean observations for each planted diversity level in the multi-species plots (details in Appendix SXI).

This test served two purposes. First, it tested whether our tradeoff surface and mechanism-based model successfully predicted positive relationships between diversity and productivity, which is a well-known property of grasslands at Cedar Creek (Tilman *et al.* 1997). Second, it demonstrated whether an empirically parameterised tradeoff surface could be used to make accurate predictions even if the identity and characteristics of individual species in mixtures are not known.

## RESULTS

Regressions that used a single monoculture characteristic (such as just  $R^*$ ) generally provided poor fits for species abundance and aboveground biomass (Table 1). One exception was  $B_{\text{mono}}^*$ , which provided the best single-characteristic fits ( $R^2 = 0.20$  for species abundances;  $R^2 = 0.70$  for aboveground biomass). Fits improved when all three monoculture characteristics were included, and improved substantially with two-way interactions among characteristics for both species abundance ( $R^2 = 0.48$ ) and aboveground biomass ( $R^2 = 0.61$ ). Three-way interactions did not significantly improve regression fits. Fits from two-way interactions improved with planted richness as a covariate ( $R^2 = 0.63$  for species abundances;  $R^2 = 0.64$  for aboveground biomass).

Relationships among characteristics fell along a clear empirical tradeoff surface, closely matching a two-dimensional plane after transformation (Fig. 1a;  $R^2 = 0.93$ ). Differences between raw and snapped characteristic values were small (Fig. 1b–d;  $0.86 \leq R^2 \leq 0.97$ ). Species clustered by functional group, with high  $R^*$ ,  $q$ , and  $B_{\text{mono}}^*$  for legumes, low values for C4 grasses, and intermediate values for C3 grasses and forbs. Matching the coexistence requirements in our mechanism-based model, species with ‘superior’ values of any one characteristic had ‘inferior’ values of one or both other characteristics ( $P < 0.005$ ; recall  $R^*$  is inversely related to competitive hierarchy). Moreover, characteristics did not correspond closely to pairwise relationships (Fig. S2), suggesting that separate information about all three characteristics was necessary for characterising tradeoffs.

Matching observations, both mechanism-based models parameterised with raw and with snapped characteristics predicted stable coexistence among the vast majority of planted species (Fig. 2). Nevertheless, models parameterised with snapped characteristics predicted greater coexistence and better matched observations, particularly in diverse mixtures. For both models, prediction error was lower for total aboveground biomass than for species abundances, and error for abundances also increased at higher diversity (Fig. 3a and b). Models fit with raw characteristics explained significant

observed variation, and had relatively high goodness-of-fit for both abundances (Fig. 3c;  $R^2 = 0.23$ ,  $P < 0.001$ ) and above-ground biomass (Fig. 3d;  $R^2 = 0.52$ ,  $P < 0.001$ ). Models parameterised with snapped characteristics had greater goodness of fit both for species abundances (Fig. 3e;  $R^2 = 0.46$ ,  $P < 0.001$ ) and total aboveground biomass (Fig. 3f;  $R^2 = 0.59$ ,  $P < 0.001$ ). For species abundances, snapped characteristics provided significantly better predictions across all richness treatments (Fig. 3a;  $P < 0.01$  for 4-species;  $P < 0.001$  for all others). For aboveground biomass, predictions from snapped characteristics were significantly better for 8- and 16-species mixtures, and when considered on average across all diversity treatments (Fig. 3b;  $P < 0.05$  8-species;  $P < 0.01$  16-species;  $P < 0.001$  all treatments).

For simulated pools of pseudo-species with characteristics sampled randomly from the tradeoff surface, predictions closely matched observations for both aboveground biomass (Fig. 4a;  $R^2 = 0.90$ ,  $P < 0.001$ ) and species abundance distributions (Fig. 4b–e;  $0.52 \leq R^2 \leq 0.95$ ,  $P < 0.001$ ). Both observed and estimated aboveground biomass increased by roughly 30% for every doubling in planted diversity. Note that higher reported  $R^2$  in Fig. 4 relative to Fig. 3 occurs because results compare means for each diversity treatment, rather than individual plots. This is necessary because the simulated species pools do not correspond directly to any planted mixture.

## DISCUSSION

Our results are consistent with the hypothesis that tradeoffs between species abilities to compete for, and access and retain nitrogen are primary determinants of coexistence and community composition among grassland plants at Cedar Creek. This conclusion is supported by three lines of evidence, discussed in detail below. First, monoculture characteristics related to these abilities fall along a constrained tradeoff surface, corresponding to well-known life history strategies. Second, mechanism-based models built around these characteristics generate accurate predictions of species abundances

without tuning predictions to match observations. Lastly, predictions improve significantly when characteristics are snapped to the nearest location on the tradeoff surface.

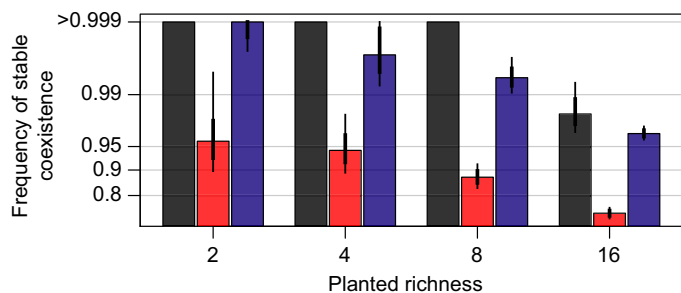
## Empirically observed tradeoffs

The highly constrained relationships observed among monoculture species characteristics provide strong phenomenological evidence of interspecific tradeoffs (Kneitel & Chase 2004; Wright *et al.* 2004; McGill *et al.* 2006; Litchman & Klausmeier 2008; Reich 2014; Evans *et al.* 2016). Furthermore, these tradeoffs correspond closely to life history strategies of functional groups at Cedar Creek (Fig. 1). Legume characteristics indicate poor nitrogen competition (low  $R^*$ ) but high aboveground tissue nitrogen (high  $B^*_{\text{mono}}$  and  $q$ ), likely resulting from nitrogen fixation, which increases nitrogen availability for the legume, but also for other nearby plants (Ranells & Wagger 1996). In contrast, characteristics identified C4 grasses as strong nitrogen competitors but poor at accessing nitrogen, consistent with experimental results showing that they competitively displace most other species in low-nitrogen environments (Wedin & Tilman 1993; Dybzinski & Tilman 2007) but are less able to access nitrogen in deeper soil or during cooler growing seasons (McKane *et al.* 1990). Lastly, C3 grasses and forbs have intermediate characteristics, indicating strategies that increase total access to nitrogen, but come at a competitive cost. For example, many C3 grasses and forbs tend to access deeper nitrogen pools and grow well in cooler seasons, but invest less in shallow root uptake during peak growing season (McKane *et al.* 1990; Fargione & Tilman 2005).

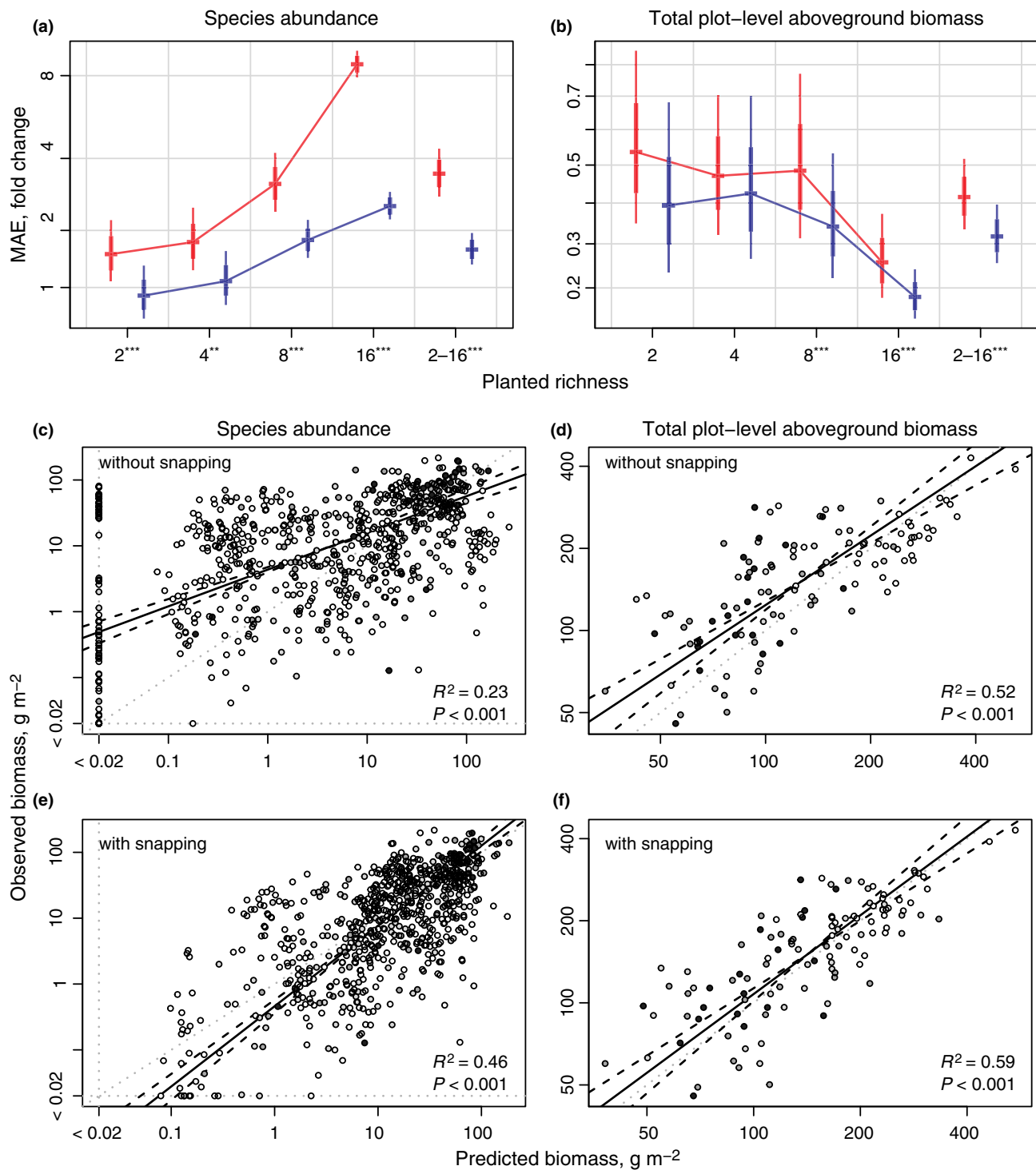
## Predictions of coexistence and community composition

Consistent with the life history strategies outlined above, species in our mechanism-based model persist in communities by investing either in competitive ability for nitrogen, or ability to access and retain a larger proportion of total available nitrogen. Furthermore, even when parameterised with raw characteristics, the mechanism-based models explained roughly as much of the observed variation in species and community abundances as did all but the most complex regression models that we tested (Table 1). Unlike the regressions, we never tuned parameters in the mechanism-based models, meaning that there is no *a priori* statistical reason to believe that predictions of coexistence, species abundance, or community biomass should match observations (Adler *et al.* 2013; Kraft & Ackerly 2014). This result therefore provides particularly strong evidence that the mechanisms and tradeoffs in our model could correspond to those that structure the observed multi-species communities (Tilman 1990; Litchman & Klausmeier 2008; Evans *et al.* 2016).

Though mechanisms and tradeoffs in our model are quite broad, potentially encompassing any strategies that allow species to access nitrogen that their competitors cannot, they nevertheless provide insight into how community composition is structured at Cedar Creek. Following Eqs (4 and 5), coexistence requires that relative fitness of inferior vs. superior competitors exceeds niche overlap (Chesson 1990, 2000;

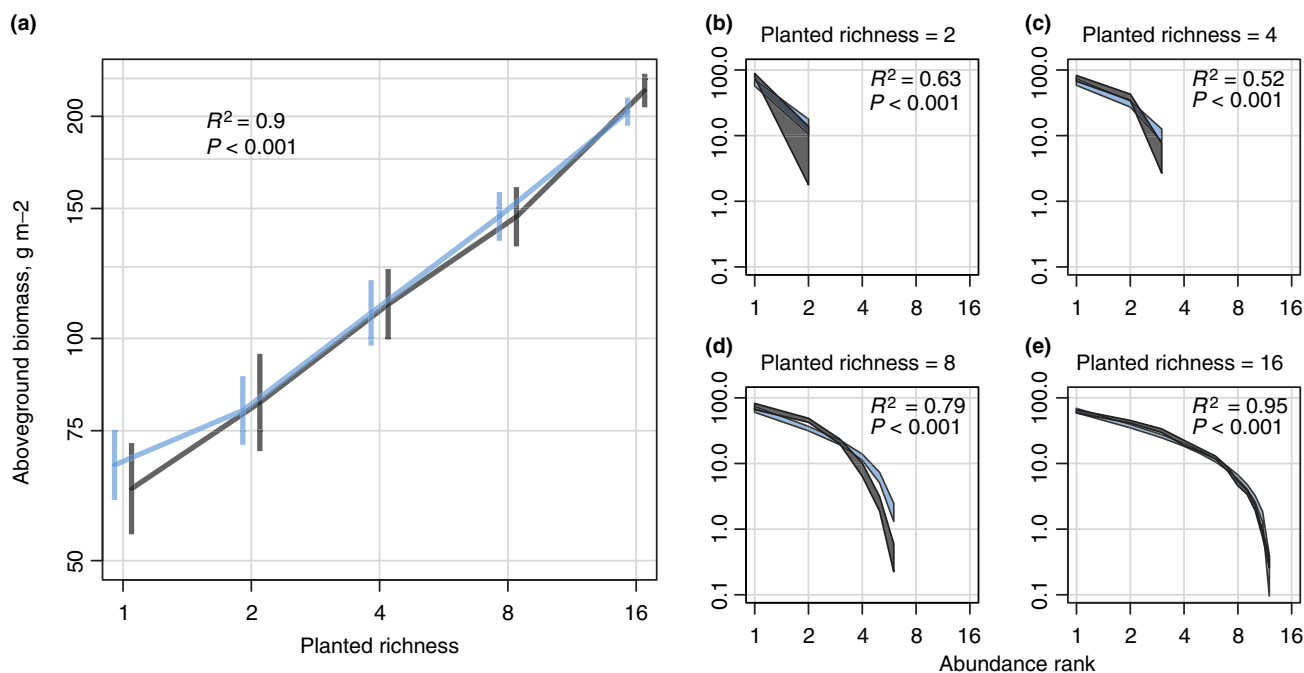


**Figure 2** Coexistence in observed communities and model predictions. Bars and intervals show mean  $\pm$  one standard deviation, and 95% confidence interval, averaged across observations or simulations. Black bars show fraction of planted species that have persisted in the multi-species plots. Red and blue bars show predictions of stable coexistence for mechanism-based models parameterised with raw and snapped characteristics respectively. Stable coexistence in these models is identified following eqn (7), as described in the main text. See Fig. S3 in the supplement for species-level results.



**Figure 3** Performance of model predictions. (a and b) Mean absolute error (MAE) for predictions of species abundances and aboveground biomass across diversity treatments ('2-16' describes average fit across all treatments). Fold change indicates the number of doublings or halvings separating predictions and observations. Red and blue lines denote fits for raw and snapped characteristics respectively. Intervals show 95% confidence interval and mean  $\pm$  one standard deviation, averaged across simulations. Asterisks by labels signify significant differences between raw vs. snapped characteristics (\* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ ). (c-f) Comparison of observed and predicted species abundances and aboveground biomass for each multi-species plot. Dark to light-coloured shapes show predictions for 2, 4, 8 and 16-species mixtures respectively. Dotted lines show lower detection limit (0.02 g m<sup>-2</sup>) and 1-1 fit; solid and dashed lines show mean and 95% confidence interval for regression slope from ranged major axis regression. In (a and b),  $P$ -values are from two-sample Wilcoxon tests; in (c-f),  $P$ -values and  $R^2$  are from major axis regression.





**Figure 4** Results for simulated species pools generated by sampling characteristics by random draws of points from the empirical tradeoff surface. Black shows results from observed multi-species mixtures; blue shows simulation results. (a) Aboveground biomass increases with planted richness. Intervals show mean  $\pm$  one standard error measured across plots. (b–e) Species abundance distributions across planted richness treatments. Shaded region shows mean  $\pm$  one standard error measured across plots. ‘Abundance rank’ sorts species from most to least abundant in each plot.  $R^2$  and  $P$ -values are from major axis regression.

Letten *et al.* 2017). Niche overlap increases as  $(q_1/q_2)B_1^*_{\text{mono}}$  grows (i.e. superior competitor biomass scaled by impact on inferior competitors), while relative fitness decreases with  $(q_1/q_2)B_1^*_{\text{mono}}$  or with decreases in  $B_2^*_{\text{mono}}$  (i.e. inferior competitor monoculture biomass). These equations therefore imply that increased nitrogen uptake by superior competitors (i.e. higher  $q_1$  or  $B_1^*_{\text{mono}}$ ) or reduced tissue nitrogen concentrations in inferior competitors (i.e. lower  $q_2$ ), are likely to reduce opportunities for stable coexistence, whereas increased monoculture biomass of inferior competitors (i.e. higher  $B_2^*_{\text{mono}}$ ) will tend to increase stable coexistence.

Though we lack evidence to identify more fine-scale mechanisms driving nitrogen partitioning, we can offer a speculative explanation based on Tilman (1994), from which we adapted our mechanism-based model. In the original model, a tradeoff between species competitive and colonisation abilities allows poorer competitors to persist by rapidly colonising new sites before superior competitors arrive. Rather than colonising physical space, species in our model can be thought of as ‘colonising’ different parts of the total available nitrogen pool across space and time. Thus, inferior competitors, which tend to have fast vegetative growth rates and rapidly colonise new sites, may be able to persist by exploiting patches and fluxes of available nitrogen before superior competitors can access them (Tilman 1994; Turnbull *et al.* 2013). Such a mechanism would be consistent with observations of plant density at Cedar Creek, where species in diverse communities fill in space left open in lower diversity mixtures (Tilman *et al.* 1997).

### Interpretations of snapping

Of the infinite number of tradeoffs among characteristics that we could have potentially observed, only a small subset allow for coexistence of many species, much less correspond to accurate predictions of species abundances. Though any tradeoff surface that included negative relationships between  $R^*$  and either  $q$  or  $B^*_{\text{mono}}$  would likely have increased predictions of coexistence by increasing total aboveground nitrogen in inferior competitors (Tilman 1994), even characteristic values snapped to the empirically observed tradeoff surface need not lead to coexistence, because both the *shape* of the surface, and the *distribution* of characteristics across that surface influence predictions of abundance and coexistence (McGill *et al.* 2006) (note species displaced by *Andropogon gerardi* or *Liatris aspera* in Fig. 1e; see Appendix SX.i in the Supporting Information for a more comprehensive proof). Thus, for predictions of coexistence, and even more so for abundance, it is difficult to explain away the improvements from snapping as a result of statistical or mathematical artefacts.

We know of two potential explanations for these improvements. Both suggest that the tradeoffs and mechanisms in our model correspond to primary determinants of community structure in the multi-species communities we consider. First, it is possible that the fitted empirical tradeoff corresponds more closely to species actual characteristics than do the raw characteristics, and observed scatter around that relationship is merely indicative of sampling noise (Purves & Pacala 2008). Though there are clearly many other characteristics and

tradeoffs that influence plant communities in other sites and systems (Chapin 1980; Wright *et al.* 2004; Reich 2014), dominance by these lower-dimensional tradeoffs could potentially be driven by a combination of physiological constraints, limiting the combinations of strategies possible for an individual organism, and ecological constraints, leading any species that fell below the tradeoff frontier to be competitively excluded (Tilman 1990, 2011).

Alternatively, if our model omits some locally influential mechanisms and tradeoffs, it could be that snapping successfully abstracts some higher-level processes (Schaffer 1981). For example, a characteristic that falls below the frontier defined by the empirical tradeoff surface (e.g. higher  $R^*$  than would be expected for a given level of  $q$  or  $B^*_{\text{mono}}$ ) may indicate energy investments in additional characteristics that make up for the deficit, but are not included in the model (e.g. efficient light acquisition). Snapping the characteristic back towards the frontier could therefore help make up for the omission. In Appendix SXI, we demonstrate that our model is indeed robust to omission of minor mechanisms by incorporating three additional mechanisms which have been shown to influence some plant communities at Cedar Creek. This feature of snapping is potentially desirable, as it could allow abstracted models to be constructed for complex systems with limited data (Purves & Pacala 2008; Sakschewski *et al.* 2016). However, it is likely limited to accounting for minor omissions. For example, there are no clear empirical tradeoffs among pairwise combinations of the characteristics we consider, suggesting that further simplification of our model would not be possible (see Fig. S2 in the supplement).

### Generalisations and broader applications

An advantage of the methods we apply is that tradeoffs are theoretically shared across coexisting species (Tilman 1990, 2011; Chesson 2000), suggesting that tradeoff surfaces parameterised using subsets of species may generate accurate predictions for the entire community (McGill *et al.* 2006; Litchman & Klausmeier 2008; Purves & Pacala 2008). Accurate predictions of species abundance distributions and community productivity from our simulated pools of pseudo-species support this hypothesis. These simulations also correctly reconstructed the shape of the positive relationship between biodiversity and productivity, according with well-known experimental results (Tilman *et al.* 1997). Again, neither the tradeoff surface nor the model guaranteed these outcomes (see Appendix SX.ii in the Supporting Information for details).

Nevertheless, there are several challenges potentially limiting the applicability of our approach. First, some systems may be sufficiently complex that they cannot be approximated with simple mechanism-based models (Clark 2010; Grimm *et al.* 2016). Similarly, available data may not always correspond to obvious empirical tradeoffs, nor to parameters in predictive mechanism-based models (Shipley *et al.* 2016). Though we may have been uniquely fortunate in being able to match long-term data to hypothesised coexistence mechanisms, there are already many successful examples of trait- or characteristic-based models (Kneitel & Chase 2004; McGill *et al.* 2006; Litchman & Klausmeier 2008; Pavlick *et al.* 2012; Rüger *et al.*

2012; Scheiter *et al.* 2013; Sakschewski *et al.* 2016), suggesting that there are likely other sites and systems in which our methods could potentially be applied.

### CONCLUSION

Our results show that information contained in empirically observed interspecific tradeoffs has the potential to inform predictive models that identify the mechanisms responsible for structuring diverse communities. Although other locations or ecosystems may have different limiting factors and a different suite of relevant characteristics, an approach like ours that is based on empirical tradeoffs and mechanism-based models may help identify those factors and improve predictions. Because many physiological tradeoffs are broadly conserved across species and locations (Wright *et al.* 2004; Reich 2014; Kunstler *et al.* 2016), there may be similar overlap in the sets of characteristics and mechanisms that determine coexistence. If this is the case, then a manageably small number of characteristics and mechanism-based models may yield strong predictions across a large range of spatial and temporal scales. The incorporation of information from tradeoffs into such models could therefore have the potential to make ecology an increasingly generalisable and predictive science.

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### Authorship

ATC, CL and DT developed the theoretical models. DT developed the tradeoff framework. ATC developed and carried out the analytical and statistical methods, and wrote the first draft of the paper. All authors contributed substantially to revisions.

## DATA ACCESSIBILITY STATEMENT

All data and source code needed to reproduce the analyses and figures presented here and in the appendix are available in the electronic supplement. All data are also available through the Cedar Creek and LTER data portals.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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