# Lifetime return on investment increases with leaf lifespan among 10 Australian woodland species

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## Summary

- Co-occurring species often differ in their leaf lifespan (LL) and it remains unclear how such variation is maintained in a competitive context. Here we test the hypothesis that leaves of long-LL species yield a greater return in carbon (C) fixed per unit C or nutrient invested by the plant than those of short-LL species.

- For 10 sympatric woodland species, we assessed three-dimensional shoot architecture, canopy openness, leaf photosynthetic light response, leaf dark respiration and leaf construction costs across leaf age sequences. We then used the YPLANT model to estimate light interception and C revenue along the measured leaf age sequences. This was done under a series of simulations that incorporated the potential covariates of LL in an additive fashion.

- Lifetime return in C fixed per unit C, N or P invested increased with LL in all simulations.

- In contrast to other recent studies, our results show that extended LL confers a fundamental economic advantage by increasing a plant's return on investment in leaves. This suggests that time-discounting effects, that is, the compounding of income that arises from quick reinvestment of C revenue, are key in allowing short-LL species to succeed in the face of this economic handicap.

## Introduction

Why do co-occurring species vary so widely in leaf lifespan (LL) (Reich *et al.*, 1997; Wright *et al.*, 2004)? The underlying causes of such a diversity of apparently successful ecological strategies must reside in the tradeoffs that equalize fitness at multiple positions along the LL continuum (Chabot & Hicks, 1982; Williams *et al.*, 1989; Reich *et al.*, 1991, 1992, 1997; Eamus, 1999; Westoby *et al.*, 2000; Wright *et al.*, 2004). Long-held hypotheses posit that investment in long-LL leaves yields a greater return for the plant in carbon (C) fixed per unit C invested ($R_C$, hereafter referred to as return on investment) (Schulze *et al.*, 1977; Chabot & Hicks, 1982; Westoby *et al.*, 2000). Under this scenario (Scenario 1 in Fig. 1), short-LL species rely on the additional proceeds obtained from quick reinvestment of C accrued to generate fitness equivalence (Westoby *et al.*, 2000). This process of reinvestment is hereafter referred to as the time-discounting effect. An alternative possibility – and one receiving recent empirical support (Mediavilla & Escudero, 2003; Kikuzawa & Lechowicz, 2006) – is that species with short- and long-lived leaves obtain equivalent return on investment,

without considering the dynamics of time discounting (Scenario 2 in Fig. 1). The implication of this result is that growth and competitive dynamics are unimportant for understanding co-occurrence of different LL strategies, because differences in LL are perfectly compensated for by covariation with other traits and factors. Establishing which of these two scenarios is true has broad implications for understanding the drivers of plant trait and species diversity.

Species differing in LL covary in an associated set of leaf traits – including leaf mass per unit area (LMA), leaf nitrogen concentration per leaf mass, net photosynthetic capacity per leaf mass, and dark respiration rate per leaf mass (Reich *et al.*, 1992, 1997, 2003; Westoby *et al.*, 2002; Wright *et al.*, 2004), known as the 'leaf economic spectrum' – the nature of which suggests an intrinsic economic advantage for long-LL strategies. To see why, consider the following equation for estimating $R_C$ (g C g$^{-1}$ C) across the lifetime of a typical leaf:

$$R_C = \frac{A_{area} \, LL}{c \, LMA} \qquad \text{Eqn 1}$$

where $A_{area}$ is the maximal C assimilation rate per unit area in young leaves, and $c$ is the carbon cost of constructing a unit of

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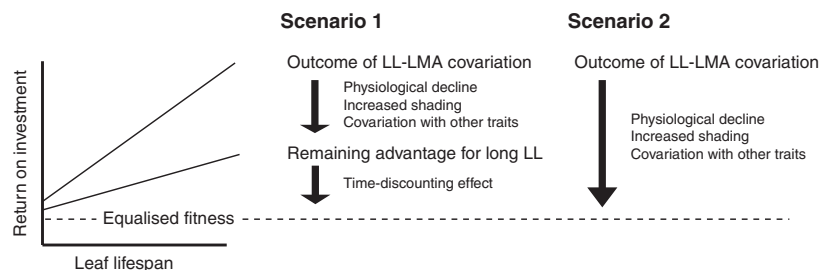
**Fig. 1** Two alternative scenarios showing how lifetime return in carbon (C) fixed per unit C invested ('return on investment') may differ for plants with different leaf lifespan (LL) strategies. The covariation of LL and leaf mass per area (LMA) across species results in a baseline positive relationship. In Scenario 1, time-discounting effects are needed to equalize fitness across species, whereas in Scenario 2 they are not.

leaf mass. Global trait databases suggest LMA scales with LL ($LMA = \alpha LL^{\beta}$), with $\beta \approx 0.5$–$0.6$, while $A_{area}$ is largely independent of LL among mixtures of co-occurring species (Wright *et al.*, 2004, 2005). This suggests a positive relationship between $R_C$ and LL of the form

$$R_C = \frac{A_{area}}{c\,\alpha} LL^{1-\beta}.$$
Eqn 2

Thus, the nature of trait-scaling relationships provides implicit support for the hypothesis that lifetime $R_C$ is greater for species with longer LL (Chabot & Hicks, 1982).

Given the apparent economic advantage of long LL, why has selection favoured such a diversity of strategies within most vegetation types around the world? Two mechanisms have been proposed that might work in favour of short-LL species, causing fitness to be equalized across the different LL strategies. Under one mechanism (Fig. 1 Scenario 2), the advantages of long LL implied by the leaf economics spectrum are offset by covariation of LL with other factors, resulting in no relationship between $R_C$ and LL. This would suggest that the C economic advantage of long-LL strategies implied by trait-scaling relationships is an illusion, arising because of a failure to consider important factors influencing C budgets. Such factors might include changes in shading, respiration by leaves and other supporting tissues, or photosynthetic capacity as leaves age, as well as covariation with other traits (Westoby *et al.*, 2000; Mediavilla & Escudero, 2003).

The other mechanism potentially favouring short-LL strategies is the time-discounting effect (Westoby *et al.*, 2000) (Fig. 1 Scenario 1). Time discounting accounts for the fact that the $R_C$ of long- and short-LL species are (by definition) calculated over different timeframes; and thus do not offer an equitable basis for comparison among species. A fairer comparison could be achieved by standardizing the duration of investment, by extrapolating the revenue streams of different species forward to some fixed time point in the future. In a growing plant, such extrapolations are achieved by reinvesting the revenue arising from the construction of leaf area into new leaf area. This process of reinvestment accelerates growth as returns compound over time, like a monetary deposit in a bank account (Blackman, 1919; Harper,

1989; Westoby *et al.*, 2000). Another way to incorporate knowledge about the process of growth and reinvestment is to bring future returns back to their present value, by discounting them at a specified 'time-discount rate' (Westoby *et al.*, 2000). Either way, short-LL species benefit more from the process of reinvestment (discounting) because their C returns are received earlier, allowing this C to be reinvested more quickly (discounted less).

These different possibilities can be formalized using an expanded equation for the return on investment received by a plant investing in a given leaf strategy:

$$R_C = \frac{A(E)}{c\,LMA} \int_0^{LL} (1 - d(t)) e^{-kt} \mathrm{d}t.$$
Eqn 3

Here $A(E)$ is the realized assimilation rate of young leaves under a given light environment ($E$), $k$ is the time-discount rate, and $d(t)$ is a function giving the relative decline in assimilation rate per area with age, incorporating changes in both leaf physiology and light environment. Under Scenario 2 in Fig. 1, estimates of $R_C$ accounting for all elements of Eqn 3 except $k$ (which is set to zero) are expected to show no relationship with LL. Under Scenario 1, a positive correlation between LL and $R_C$ is expected when time-discounting effects are omitted (Fig. 1). Although Eqn 3 allows for a complete estimate of $R_C$, considerable effort is required to estimate all the relevant components, and thus this has never been done.

At least two studies suggest the benefits of long LL are entirely offset by covariation with other factors (Fig. 1 Scenario 2). Among 12 co-occurring Mediterranean woody species, Mediavilla & Escudero (2003) found a greater age-related decline in photosynthetic capacity among long-LL species, offsetting the advantage of long LL. Kikuzawa & Lechowicz (2006) took a different approach but arrived at a similar conclusion. They compared data for 26 species compiled from the literature from a variety of sites, biomes and climate zones and combined this with a model that factored in the fraction of each day that might not be conducive to maximum photosynthesis and the fraction of each year that might not be conducive to maximum photosynthesis, as well as the decline in photosynthetic capacity with leaf age. They found considerable scatter in lifetime revenue at any LL but no relationship between lifetime revenue and LL.

As yet no study has directly measured the time-discounting effect in real systems, but at least two studies provide preliminary evidence indicating its importance in equalizing the fitness of different strategies. Based on estimates of maximum $R_C$ obtained from trait data, Westoby *et al.* (2000) estimated the value of the time discount rate needed to offset the advantages of long LL, with values ranging from 0.05 to 0.18 for different systems (i.e. all > 0). In another study, Selaya & Anten (2010) compared $R_C$ among early and late successional species in a tropical forest secondary succession. Although their calculations do not explicitly account for the process of reinvesting early returns, the outcomes of this reinvestment may still be seen in their results. They found that individuals from later successional species (with long LL) experienced a sharper decline in light environment as they recovered after disturbance, presumably because of the rapid growth rates of short-LL species, made possible by the time-discounting effect. Moreover, this decline was strong enough to offset the intrinsic economic advantage of long-LL species, so that $R_C$ was unrelated to LL. Thus time-discounting effects, including their competitive outcomes, may equalize fitness across species.

Overall, however, a surprisingly small number of studies have attempted to estimate quantitatively the lifetime C revenue of a leaf through any means (Kikuzawa, 1991; Ackerly, 1999; Eamus, 1999; Givnish, 2002; Kikuzawa & Lechowicz, 2006; Oikawa *et al.*, 2006); and even fewer have made time-integrated life cycle analyses of the costs and benefits of extended LL (Westoby *et al.*, 2000; Mediavilla & Escudero, 2003; Kikuzawa & Lechowicz,

2006; Selaya & Anten, 2010; McMurtrie & Dewar, 2011). A survey of the empirical information included in these studies shows that each had only a modest capacity to estimate $R_C$ (Table 1). Moreover, none of the studies listed in Table 1 included direct measurement or simulation of physiology over the lifespan of specific leaves or leaf sequences.

Given these various sources of uncertainty, we present here an additional study of $R_C$ among co-occurring Australian woodland species. Our approach complements previous publications (Table 1 and others) by combining measurements and models to estimate $R_C$ for leaves of 10 co-occurring woody plants in Australia. We measured in the field a variety of physiological and light environmental attributes for leaves varying in age and position for each species. Although our study is also not a complete accounting of $R_C$ (see Table 1 and details later), it does make several steps forward in understanding the significance of LL by providing direct measurements of changes in the degree of shading and leaf physiology with leaf age, using measured photosynthetic light response curves and dark respiration. In addition, the methods used allow us to separate out the various factors that might compensate for the intrinsic advantages of long LL (Table 2). In a companion paper we examined the factors that control the decline in C revenue as leaves age (Reich *et al.*, 2009). In the current paper we test whether these factors are sufficient to offset the intrinsic advantages of long LL implied by trait-scaling relationships in the absence of time-discounting effects (i.e. Scenario 2 in Fig. 1), as suggested by

**Table 1** Overview of studies calculating $R_C$ in relation to leaf lifespan (LL)

| Vegetation type | Mediavilla & Escudero (2003) Mediterranean trees | Kikuzawa & Lechowicz (2006) Woody species from a mix of climates | Selaya & Anten (2010) Tropical rainforest | This paper Temperate woodland |
|---|---|---|---|---|
| **Calculation of $R_C$** | | | | |
| Number of species studied | 12 | 26 | 8 | 10 |
| Study restricted to co-occurring species | Y | – | Y | Y |
| $R_C$ estimated across lifespan of a typical leaf | – | Y | Y | Y |
| Time-discounting effect included | – | – | – | – |
| **Factors included in calculation of $R_C$** | | | | |
| Local light environment | – | – | E | Y |
| Increased shading as leaf gets older | – | – | E | Y |
| Light measured and applied to a light-response curve | – | – | E | Y |
| Leaf lifespan (LL) | E | L | E | E |
| Construction cost of leaf in C | E | L | E | E |
| Photosynthesis of young leaves | E | L | E | E |
| Decline in photosynthetic capacity with age | E | – | – | E |
| Dark respiration of leaves, including through the night | – | – | – | E |
| Respiration in stems and roots | – | – | – | – |
| Cost of constructing sapwood and fine roots in association with constructing the leaf | – | – | – | – |
| Carbon cost of acquiring N and/or P for the leaf added to LMA for estimating initial investment cost | – | – | – | – |
| Effect of factors other than light on photosynthesis | – | – | – | – |

Y, yes, measured along a specific leaf sequence for which $R_C$ was calculated; E, estimated, that is, measured for the vegetation, but not along a specific leaf sequence for which $R_C$ was calculated; L, obtained from the literature; –, not included.

**Table 2** Overview of the YPLANT simulations run, and resulting relationships with leaf lifespan (LL) across 10 Australian woodland species for two measures of performance: lifetime revenue and return on investment ($R_C$)

| Simulation | Covariation of LL with leaf mass per area and assimilation rate per area | Changes in leaf orientation along leaf sequence | Changes in within-branch shading along leaf sequence | Changes in beyond-branch shading along leaf sequence | Changes in photosynthetic capacity shading along leaf sequence | Light niche differentiation | Night respiration | Lifetime revenue (g C m$^{-2}$) | | | | Return on investment (g C g$^{-1}$ C) | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | $a$ | $b$ | $r^2$ | $P$ | $a$ | $b$ | $r^2$ | $P$ |
| 1 | * | * | | | | | | 2.68 | 1.038 | 0.64 | 0.006 | 0.615 | 0.793 | 0.58 | 0.010 |
| 2 | * | * | * | | | | | 2.58 | 1.016 | 0.62 | 0.007 | 0.520 | 0.771 | 0.57 | 0.011 |
| 3 | * | * | * | * | | | | 2.57 | 0.978 | 0.61 | 0.007 | 0.508 | 0.734 | 0.59 | 0.010 |
| 4 | * | * | * | * | * | | | 2.48 | 1.014 | 0.65 | 0.005 | 0.414 | 0.770 | 0.65 | 0.005 |
| 5 | * | * | * | * | * | * | | 2.52 | 0.784 | 0.58 | 0.011 | 0.459 | 0.540 | 0.65 | 0.005 |
| 6 | * | * | * | * | * | * | * | 2.37 | 0.703 | 0.32 | 0.091 | 0.311 | 0.459 | 0.23 | 0.159 |

Reported here are the results of linear regressions of the form $\log_{10}(Y) = a + b \log_{10}(\text{LL})$, where $Y$ is either lifetime revenue or $R_C$.

previous studies (Mediavilla & Escudero, 2003; Kikuzawa & Lechowicz, 2006).

## Materials and Methods

In this study we quantify two key measures of success that are useful for comparing across species. First, we estimate the C revenue obtained from a typical leaf throughout its lifetime (hereafter referred to as lifetime C revenue, g C m$^{-2}$); this corresponds to the numerator in Eqn 3. Second, we estimate the return on investment $R_C$ (g C g$^{-1}$ C) for the plant, given by the ratio of lifetime C revenue to the C construction cost of the leaf (Eqn 3). Both estimates are made excluding time-discounting effects, that is, with $k = 0$. These estimates were made using a combination of physiological measurements, three-dimensional (3D) digitizing of entire leaf sequences, and hemispherical photography characterizing branch light environments. Our field methods are only summarized here, as they are described in full elsewhere (Reich *et al.*, 2009; Pearcy *et al.*, 2011).

### Study sites and species

The study site was Ku-ring-gai Chase National Park (33º41′38″S, 151º8′35″E), Sydney, NSW, Australia. The vegetation is fire-prone temperate woodland with a high diversity of shrub species under an open eucalypt canopy, growing on infertile soils derived from Hawkesbury Sandstone parent material. Average annual rainfall is 1220 mm distributed throughout the year and mean daily temperatures are 22 and 13°C in summer and winter, respectively. Further details about the study site are given in Wright *et al.* (2001). Ten woody plant species were chosen to span a range of LL. Eight were shrubs – *Acacia suaveolens* (Sm.) Willd., *Banksia marginata* Cav., *B. oblongifolia* Cav., *Eriostemon australasius* Pers., *Grevillea buxifolia* (Sm.) R. Br., *Hakea dactyloides* (Gaertn.) Cav., *Lambertia formosa* Sm., *Persoonia levis* (Cav.) Domin – and two were woodland trees – *Corymbia gummifera* (Gaertn.) K.D. Hill & L.A.S. Johnson and *Eucalyptus haemastoma* Sm. Five or six individual plants (1–4 m tall) were chosen per species. We sampled the uppermost leading branch (i.e. shoot) on each plant. All branches were in semi-open conditions, with their canopy openness (% of total incoming photon flux density) ranging from 28 to 50% among species, and averaging 36% for all 53 branches.

### Estimating lifetime C revenue for a typical leaf from each species

To estimate lifetime C revenue of each of our 10 study species, we employed a space-for-time substitution implemented along leaf sequences, with ages of individual leaves estimated from leaf position along the shoot combined with past estimates of mean LL taken from Wright & Westoby (2002). 3D digitizing of branch architecture and measurements of leaf physiological performance were then combined within the architectural model YPLANT (Pearcy & Yang, 1996; Falster & Westoby 2003) to estimate daily light interception and C gain across the lifespan of a typical leaf in each species (for details on equipment, see Pearcy

*et al.*, 2011). YPLANT uses a virtual 3D reconstruction of the plant to estimate light interception and potential carbon gain for different sample periods throughout a single day and integrated across entire days. An embedded solar model simulates movement of the sun across the sky for a particular location and date. The density of diffuse and direct light photon fluxes on the surface of each leaf is determined by its orientation relative to the sun, the amount of shading from surrounding vegetation (described in a hemispherical canopy photo), and the amount of self-shading within the digitized plant (calculated using a ray-tracing algorithm). Photosynthetic rates are then estimated based on the simulated light interception and measured light-response curves, assuming water availability does not limit stomatal aperture.

Hemispherical photographs were taken at several distances down the sequence, but with the branch itself removed from field of view. This enabled the shading from all surrounding vegetation to be estimated along the leaf sequence, and cumulative revenue to be calculated across the lifespan of a typical leaf on each branch.

Field photosynthesis (both maximum capacity and light-response curves) and respiration data were collected for leaves across the leaf position/age sequence on each branch (Reich *et al.*, 2009). The decline in maximum light-saturated photosynthetic rates (maximum capacity) per unit area with leaf age was characterized using 509 measurements from 151 plants (three or four leaves per branch per plant), while photosynthetic light-response curve parameters were characterized for 104 individual leaves (three to four per species for three or four leaf position classes) among the 10 species (see Reich *et al.*, 2009 for further details).

YPLANT was used to estimate light interception and C gain across eight different days spread throughout the year, which were then integrated to give an average daily rates (Pearcy & Yang, 1996). Different YPLANT simulations were run to include different factors affecting light interception and branch-level C gain, including changes in leaf orientation, within-branch shading, beyond-branch shading, and photosynthetic capacity along the leaf sequences, and differences in average light environment and night-time respiration rates, in an additive fashion (Table 2). The latter two effects are equal for all leaves on a branch, whereas the other effects increase with leaf age. Based on these simulations, we estimated $R_C$ as per Eqn 3, accounting for all elements except the time discount rate $k$ (set to zero).

To compare return on investment among species, we used branch-level simulation data to estimate the lifetime C revenue of a typical leaf of each species under two different light environments: a common incident daily light of 20 mol m$^{-2}$ d$^{-1}$, and under the average light environment experienced by the species. Within each species, lifetime C revenue was positively related to branch light environment (as expected), quantified here as average incoming irradiance just above each individual branch (mol m$^{-2}$ d$^{-1}$, photosynthetic photon flux density). Fig. 2 shows the observed patterns for one of the branch-level C gain simulations, which incorporates loss of revenue through increased shading down leaf age sequences and through physiological decline in photosynthetic capacity. Estimates of lifetime C revenue under a standard light environment were obtained by interpolating along
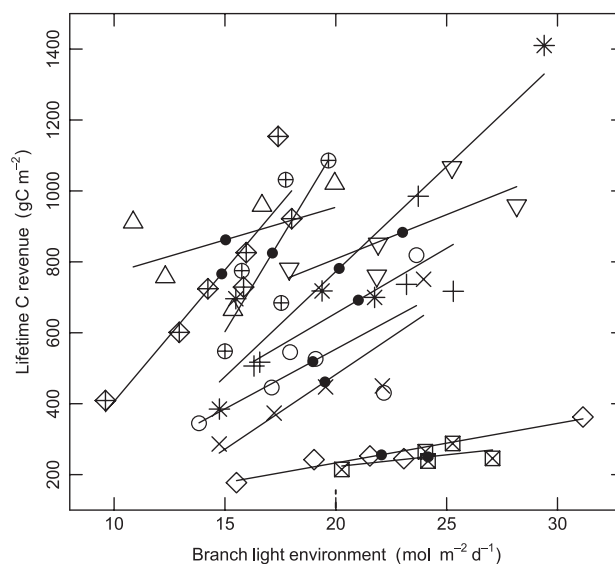


**Fig. 2** Relationship between simulated lifetime revenue under simulation four (see Table 2 for details) and the light environment at top of each branch. Each symbol and linear regression line corresponds to a different species. The average $r^2$ of these relations was 0.64 (range 0.20–0.95). The mean branch light environment and corresponding revenue for each species is indicated by a closed circle.

regression lines fitted between branch light environment and revenue estimated under a given simulation – such as those represented in Fig. 2 – to a common incident daily light of 20 mol m$^{-2}$ d$^{-1}$. This process was repeated to estimate lifetime C revenue under simulations 1–4 (Table 2), enabling the various factors influencing changes in C revenue to be studied, without being confounded by differences in branch light environment. Nine of the 10 species had at least one individual in the range of observed values close to the interpolation point of 20 mol m$^{-2}$ d$^{-1}$. The 10th species had a maximum incident daily light of 17 mol m$^{-2}$ d$^{-1}$ and a linear relation of lifetime revenue to light environment, suggesting that our simulation at 20 mol m$^{-2}$ d$^{-1}$ should be realistic.

Fitted regressions for simulation four were then used to estimate lifetime revenue under the average light environment experienced by each species (referred hereafter to as light niche differentiation). Simulations 5 and 6 thus incorporate the effects of light niche differentiation.

Our simulations are subject to several limitations, as discussed by Reich *et al.* (2009). In brief, we do not consider differences between diffuse and direct light-driven photosynthesis, variation in leaf absorbance, stress-induced stomatal closure, or other water-use considerations that impact plant C gain, despite the recognized importance of most or all of these factors (Sperry *et al.*, 2002; Brodersen *et al.*, 2008). There is, as yet, no general comprehensive physiological model that handles all these factors well or that has been implemented across leaf sequences.

### Estimating C return on investment for a typical leaf from each species

The C construction costs of foliage (gC m$^{-2}$) were estimated from measured values of LMA (for young leaves) using a

conversion factor obtained from data published by Villar & Merino (2001). In that study, the total cost of building a unit of leaf (g glucose $g^{-1}$ leaf) was estimated using calorimetric methods along with LMA for 121 species. Additional analysis of their data shows a tight relationship between C construction cost per unit leaf area and LMA ($r^2 = 0.98$). The slope of this relationship (1.04) is very close to 1.0, supporting the use of an isometric relationship in Eqns 1–3. Forcing a slope of 1.0 through the data yielded a conversion factor of 1.53 g glucose $g^{-1}$ leaf. Noting also that each g of glucose contains 0.4 g of C, the parameter $c$ in Eqns 1–3 is given by $c = 1.53 \times 0.4 = 0.612$.

It is also worth asking whether our results would differ if the 'investment' component of Eqn 3 was measured in a currency other than C, such as nitrogen (N) or phosphorus (P). This may be relevant in low-nutrient systems where there is a premium on nutrient-use efficiency (Chapin, 1980; Oleksyn *et al.*, 2003; Reich *et al.*, 2003). To address this concern, we used our dataset to calculate the return in C fixed per unit N invested (g C $g^{-1}$ N) as

$$R_N = \frac{A(E) \int_0^{LL} (1 - d(t))dt - c \times LMA}{N_s} \qquad \text{Eqn 4}$$

where $N_S$ is the nitrogen content per unit area in senesced leaves. Eqn 4 is similar to Eqn 3, except that the investment component is quantified as the amount of nutrients used in leaf construction rather than C; the C cost instead being subtracted from the revenue stream. A similar calculation gives lifetime return in C fixed per unit P invested ($R_P$). We calculated $R_N$ and $R_P$ for our 10 species by combining data for lifetime return in simulation 6 (Table 2), together with measurements on the N and P content of young leaves, and published data for these species on the %N and %P resorbed before leaf loss (Wright & Westoby, 2003; see Supporting Information, Notes S1, for details).

### Statistical analysis

Ordinary least-squares (OLS) linear regression was used to quantify relationships between LL and lifetime revenue and return on investment under the different simulations. As additional factors affecting $R_C$ were added, we looked for changes in the slope of the relationship with LL. Our null hypothesis was that all simulations would show a positive relationship between $R_C$ and LL,

because time-discounting effects were omitted in the calculation of $R_C$. The alterative hypothesis was that there would be no relationship (slope of zero) between LL and $R_C$ in the simulations incorporating all additional factors (Fig. 1). OLS linear regression is most suitable for this analysis because the fitted slope approaches zero as the $r^2$ decreases, whereas this is not the case in alternative line-fitting techniques such as standardized major axis.

### Results

The 10 species ranged in LL from 1.01 to 3.79 yr (Wright & Westoby, 2003). LMA was positively correlated with LL, while maximum assimilation rate per unit leaf area, dark respiration rate per unit leaf area, leaf nitrogen content per unit leaf area and leaf phosphorus content per unit leaf area for young leaves were only weakly correlated with LL (Table 3), as generally observed both locally and globally (Reich *et al.*, 1997; Wright *et al.*, 2004). Although the correlation between LL and LMA was not significant, this is not unexpected given the small number of species sampled. Moreover, the relationship is characterized by a moderate $r^2$, consistent with other studies in this vegetation (Wright & Westoby, 2003). Species varied significantly in light environment (ANOVA, $P = 0.002$), with average light environment showing a significant negative correlation with LL (Table 3).

Return on investment ($R_C$) was greater in species with longer LL for all six simulations (Fig. 3). Fig. 3 shows the effects of adding changes down the leaf sequence in total shading (Fig. 3b) and declines in photosynthetic capacity (Fig. 3c) to the baseline simulation (Fig. 3a), which only incorporates the effects of trait correlations and leaf orientation on $R_C$. Incorporating each of these factors decreased the average value of $R_C$, but did not offset the intrinsic advantage of longer-lived leaves (i.e. there was a change in intercept but no change in slope, Fig. 3f). Similar results – that is, a change in intercept of fitted regressions but no change in slope – were obtained when lifetime C revenue was related to LL (Table 2). The slopes of these relationships (for lifetime revenue) were close to 1.0 and, on average, 0.244 units higher than those relating $R_C$ to LL (Table 2). Slopes close to 1.0 indicate that lifetime C revenue is proportional to LL and not offset by any of the additional factors included in simulations 1–4. The flatter slope found between $R_C$ to LL shows the effect of dividing by LMA in the calculation of $R_C$ (Eqn 1), thus incorporating the underlying correlation of LL with LMA (Table 3).

**Table 3** Relationship of leaf lifespan (LL) with other leaf traits and average branch light environment across 10 Australian woodland species

| Trait | a | b | $r^2$ | P |
|---|---|---|---|---|
| Leaf mass per area (LMA) | 2.28 | 0.244 | 0.22 | 0.17 |
| Photosynthetic capacity per unit area ($A_{area}$) | 0.99 | 0.087 | 0.01 | 0.74 |
| Dark respiration rate per unit area | 0.088 | 0.035 | 0.00 | 0.91 |
| Nitrogen content per unit area | 0.29 | −0.002 | 0.00 | 0.99 |
| Phosphorus content per unit area | −1.22 | −0.084 | 0.02 | 0.71 |
| Branch light environment (E) | 1.36 | −0.24 | 0.44 | 0.37 |

All traits were measured on young leaves. Reported here are the results of linear regressions of the form $\log_{10}(Y) = a + b \log_{10}(LL)$.
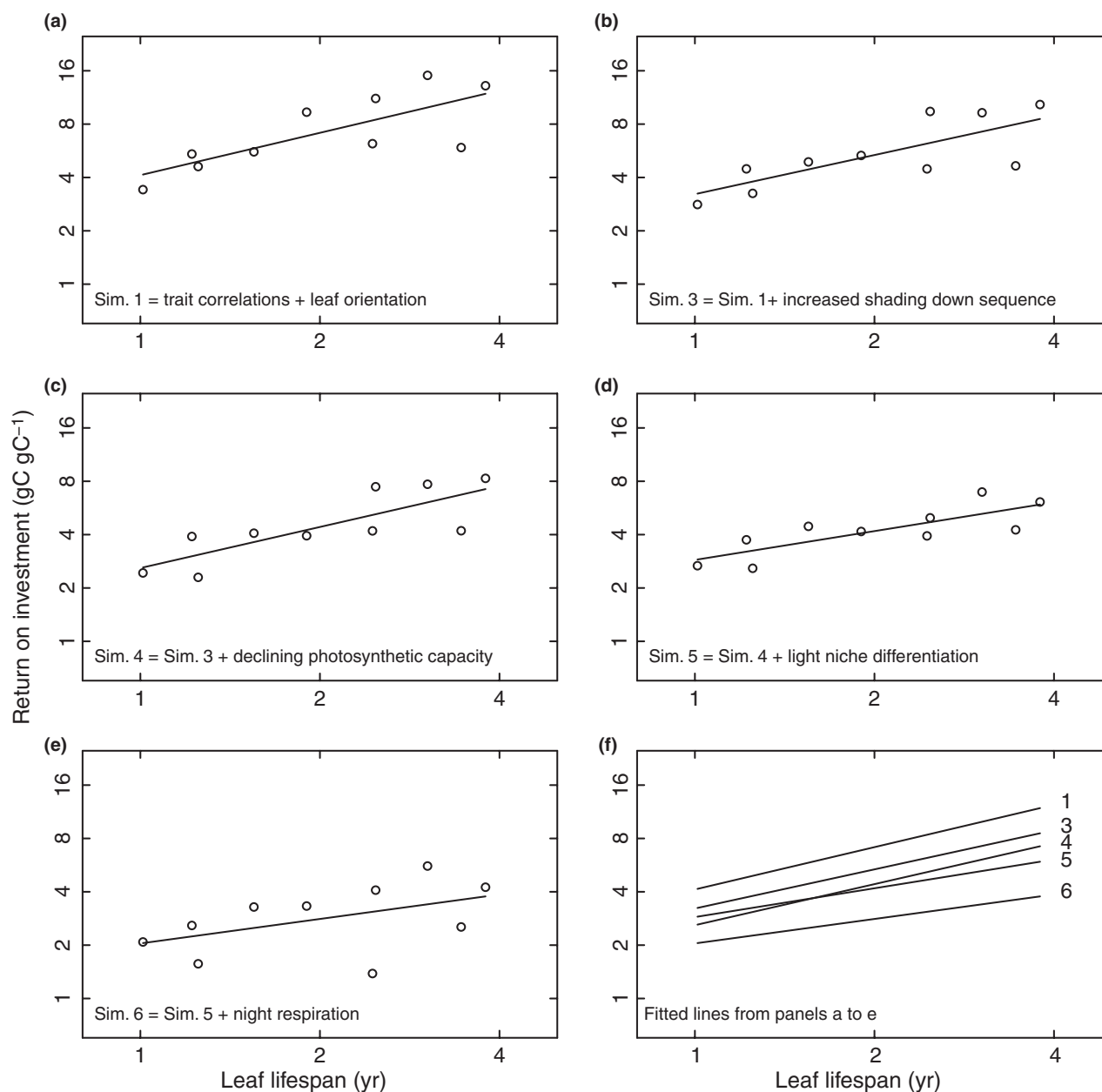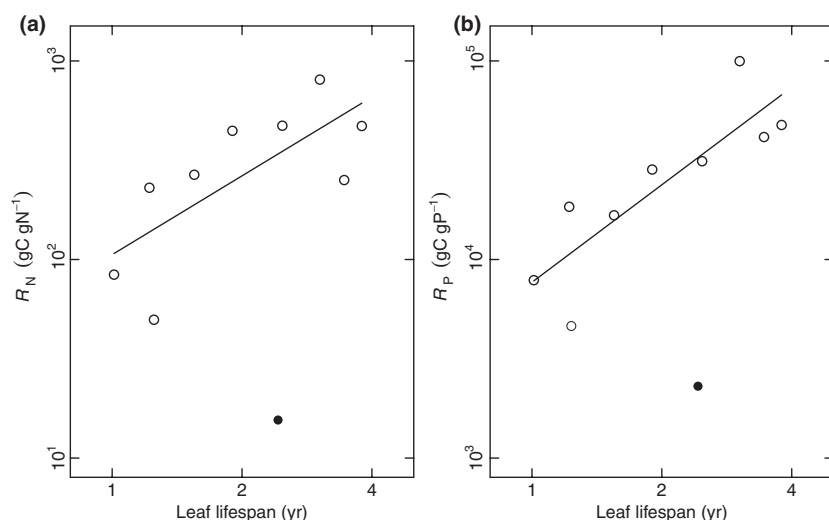
**Fig. 3** Relationship between lifetime return on investment ($R_C$) and leaf lifespan for a series of simulations; each introducing a new factor affecting $R_C$. Factors are introduced in an additive way, as outlined in Table 2. For comparison, (*f*) shows the regression lines from all previous panels. See Table 2 for details on the fitted regression lines. Sim., simulation.

These results show that incorporating changes in within-branch shading, beyond-branch shading and photosynthetic capacity shading along leaf sequences did not offset the intrinsic advantages of longer LL on $R_C$. Adding differences caused by light niche differentiation, however, did decrease the slope of the relationship between $R_C$ and LL (Fig. 3d,f). This occurred because species with shorter-lived leaves tended to occur in higher light (Table 3). Nonetheless, species with longer-lived leaves still retained a significant advantage in $R_C$, even after accounting for light niche differences.

Adding the effects of night-time respiration also did not alter the slope of the relationship between LL and $R_C$ (Fig. 3e,f), but

did decrease the strength of the relationship to make it nonsignificant (Table 2). Respiration rate was not significantly related to LL (Table 3), so the change in significance reflects the increased amount of noise in the data, rather than a systematic change in relation to LL.

Consistent with the pattern shown by $R_C$, both $R_N$ and $R_P$ showed a strong relationship to LL (Fig. 4). In other words, quantifying investment in units of nutrient did not alter the tendency in our data for long-LL species to receive a greater return on investment. However, note that these relationships were significant only when the single nitrogen-fixing species was omitted (Fig. 4).

**Fig. 4** Relationship between leaf lifespan (LL) and simulated lifetime return in carbon (C) fixed per unit nitrogen ($R_N$) and phosphorus ($R_P$) invested for 10 Australian woodland evergreen species. Shown are regression lines of the form $\log_{10}(Y) = a + b \log_{10}(LL)$, where $Y$ is either $R_N$ or $R_P$, with parameters: (a) $a = 2.02$, $b = 1.31$, $r^2 = 0.53$, $P = 0.026$; (b) $a = 3.88$, $b = 1.63$, $r^2 = 0.72$, $P = 0.003$. Both lines were fitted excluding the nitrogen-fixing species *Acacia suaveolens*, shown using a closed circle.

## Discussion

Our estimates of return on investment were found to increase with LL among this set of 10 Australian woodland species. This finding supports early hypotheses and results based on 'snapshot' trait values (Schulze *et al.*, 1977; Chabot & Hicks, 1982; Reich *et al.*, 1991, 1992; Westoby *et al.*, 2000) but disagrees with other studies (Mediavilla & Escudero, 2003; Kikuzawa & Lechowicz, 2006; Selaya & Anten, 2010). Moreover, our results suggest a central role for time-discounting effects in equalizing fitness across species. Although our estimates of lifetime C revenue have a stronger basis in measurements than many, if not all, previous estimates of $R_C$ (Table 1), considerable uncertainties remain. Studies of $R_C$ thus far have been based on small and idiosyncratic sets of species; each considering only a limited number of factors, leaving open the possibility of unmeasured factors altering conclusions; and no study of $R_C$ has directly quantified the strength of time-discounting effects (Table 1). In the following, we discuss each of these uncertainties, in light of the results from current and previous studies, and the implications for our understanding of LL variation in plant communities.

### The challenge of testing ecological theory with small species sets

With the accumulation of large trait databases it is becoming common to encounter comparative papers with 100s or 1000s of data points (Reich *et al.*, 1997; Wright *et al.*, 2004). However, studies involving more detailed measurements, such as this one, remain limited to tens of species. In some ways, detailed studies provide greater accuracy and insight. However, the inevitably small sample sizes that are associated with making detailed measurements also reduce certainty about the inferences drawn.

In a study of 12 Mediterranean woody species, Mediavilla & Escudero (2003) analysed changes in the maximum rate of C assimilation per unit leaf mass ($A_{mass} = A_{area} / LMA$) across the lifespan of leaves in each species. They found that $A_{mass}$ averaged across the leaf lifetime was related to LL with a log–log slope

close to $-1$. They interpreted the slope of $-1$ as suggesting that $R_C$, given by the product of $A_{mass}$ and LL (Eqn 1), would be independent of LL (slope $\approx 0$). Their study is similar to ours in that both incorporate changes in photosynthetic capacity with age. Unlike their study, however, trait intercorrelation and age-related changes in photosynthetic capacity among our species did not offset the advantages of longer LL for $R_C$ (Fig. 3).

The main reason our results differ from those of Mediavilla & Escudero (2003) is the strength and nature of the observed cross-species correlations among traits. Specifically, Mediavilla & Escudero (2003) found a strong negative correlation between assimilation per unit area and LL ($r^2 = 0.39$), whereas the relationship was absent in our study ($r^2 = 0.01$; Table 3). The negative correlation reported by Mediavilla & Escudero (2003) implies an additional advantage for species with short LL, compared with our system, resulting in a different conclusion.

It is plausible that the differences in trait correlation seen in our study compared with that of Mediavilla & Escudero (2003) arise from fundamental differences in the ecology of the two study systems. For example, rainfall is more evenly distributed across seasons in our system, compared with the Mediterranean system studied by Mediavilla & Escudero (2003), potentially benefiting long-LL strategies more. However, observed differences may also reflect the small and idiosyncratic sets of species chosen for study. Wright *et al.* (2005) and Reich *et al.* (2010) have shown that although correlations among leaf traits converge to some asymptotic value as increasing numbers of species are sampled ($\approx$ 20–200 depending on the relationship), studies including only few species may show a variety of patterns in slope and $r^2$. Our study only included 10 species, while that of Mediavilla & Escudero (2003) included 12. Together these two studies bracket the relationship between assimilation per unit area and LL observed in a global dataset with many more species ($r^2 = 0.13$ $n = 512$; Wright *et al.*, 2004).

One way to increase sample size, and thus certainty about the nature of trait correlations, is to pool available measurements across different studies. Taking this approach, Kikuzawa & Lechowicz (2006) modelled $R_C$ as the product of $A_{mass}$ (averaged over the lifetime), LL, the part of the day the leaf functions to

maximum capacity, and the fraction of LL that is favourable for photosynthesis. Their 26 species were drawn from several different studies and from sites in different biomes. However, one may also question the worth of pooling data across sites when comparing $R_C$ across species. There are good theoretical reasons why coexisting species should be equivalent in some measure of fitness, but the same does not apply when comparing species from differing environments. The conclusions of Kikuzawa & Lechowicz (2006) may also be influenced by the nature of the available data. If one separates their data in their Fig 1 into species with short LL (<1 yr) and those with long LL, one might reasonably conclude that there were opposite patterns for those two groups rather than that there was no overall pattern to the data. Therefore, the validity of pooling of data across sites should be critically evaluated in relation to the hypothesis being addressed.

So how can future studies increase certainty about the relationship of LL to $R_C$, balancing the competing demands of detailed measurements and increased sample size? Our results show that insights into the relationship between LL and $R_C$ obtained from simple trait measurements are reliable and commensurate with those obtained from more detailed modelling of lifetime revenue. Incorporating additional architectural and physiological changes into our simulations did not alter the baseline relationship between LL and $R_C$, only the absolute values of $R_C$ (Fig. 3f). At the same time, our results also suggest that future studies should measure light environment when estimating $R_C$. Differences in branch light environment had a large influence on estimated $R_C$ (Fig. 2), and significantly altered the cross-species relationship between LL and $R_C$ (Fig. 3f). Quantifying the light environment of a branch requires some additional effort, but is still easier than digitizing its 3D structure. By combining measurements of traits and light environment, researchers may be able to estimate accurately the relationship between LL and $R_C$ for larger sets of coexisting species than was possible in the current and previous studies (Table 1).

## Deciding which factors to include as potential covariates of LL

Intertwined with the question of how many species to sample and with what detail is a decision about which variables to measure as potential covariates of LL.

We did not measure several factors that probably affect lifetime C revenue (Table 1), such as water relations/hydraulic feedbacks and the costs of constructing and maintaining stems and roots. Although inclusion of additional factors may adjust estimates of $R_C$, their inclusion would only alter our conclusions if this adjustment applied more intensely to species at one end of the leaf economics spectrum than another. For instance, low daytime temperatures might reduce C assimilation rates in cooler seasons (an effect not included in our model), but this would not affect our qualitative conclusions unless the amount of reduction differed systematically between species with long and short LL. Indeed, our results show how measurement of some additional factors, such as within-branch shading and age-related decline in photosynthetic capacity, alter estimated values of $R_C$ without

affecting its relationship to LL (Fig. 3). Thus, decisions about which variables to measure should be driven by specific hypotheses, rather than a list of what is missing.

Existing theory suggests at least one variable that systematically alters the relationship of $R_C$ to LL: light environment. In our study, branch light environment was correlated with LL, partially offsetting the advantages of having long LL. The vegetation we studied is characterized by a relatively open canopy, potentially limiting the strength of shading effects. However, a similar study along a successional gradient in a secondary, tropical forest shows a much stronger effect (Selaya & Anten, 2010). Like us, Selaya & Anten (2010) measured leaf physiological traits and combined these with a light interception model to estimate lifetime revenue. But in contrast to our results, they found the magnitude of decline in light interception with leaf age to be tightly coordinated with LL, such that the leaves of species with long LL suffered a greater decline in revenue with age. Ultimately this led to the absence of any relationship between LL and $R_C$.

In tropical rainforests, species at the short-LL end of the leaf economics spectrum are typically found in better light environments than those species with a slower leaf strategy (Williams et al., 1989; Reich et al., 1995; Poorter & Bongers, 2006). Thus we might expect the results reported by Selaya & Anten (2010) to be repeated at most tropical forest sites. By contrast, species growing in more open Mediterranean systems tend to be less differentiated in growth strategy and microsite. The broader question is whether individuals with longer LL consistently occur in shadier microsites across a range of vegetation types?

It is also possible that the costs of constructing and maintaining stem and root tissues, unmeasured in the current study, differ systematically with LL, in a fashion that counters the economic advantages of long LL. For example, the roots and/or stems of short-LL (high LMA) species may be cheaper to build and maintain. However, evidence thus far suggests LL and LMA are only weakly associated with other stem and root traits, if at all (Craine et al., 2005; Wright et al., 2010). Thus it seems unlikely that these effects would be sufficiently strong to counter the higher $R_C$ of long-LL species.

The cost of acquiring and retaining nutrients within leaves – primarily N – is also thought to influence the evolution of LL (Chapin, 1980; Chabot & Hicks, 1982; Reich et al., 1995; Givnish, 2002; Reich et al., 2003; Oleksyn et al., 2003; McMurtrie & Dewar, 2011). In this regard, our results support the long-standing idea that species with long LL yield a greater return in carbon fixed unit N or P invested (Fig. 4), and are therefore more likely to be favoured in nutrient-poor habitats (Chabot & Hicks, 1982; Givnish, 2002). Most theory about the influence of nutrient uptake on LL, however, is aimed at explaining differences in LL among sites; much less so the range of LL strategies observed within a single site.

A recent model by McMurtrie & Dewar (2011) makes some progress in this regard. Based on the hypothesis that plants adjust their LMA and leaf N to maximize total lifetime C revenue of leaves growing in different light and nutrient supply environments, McMurtrie & Dewar (2011) recovered the main trait correlations encompassed by the leaf economic spectrum. Moreover, their

model predicts an explicit relationship between $R_C$ and the fraction of N resorbed before leaf death (their eqn C7), suggesting a potential link between LL and N resorption. Unfortunately, available data sets – including one from our study site – suggest no such relationship exists (Escudero *et al.*, 1992; Wright & Westoby, 2003). Also, species in McMurtrie and Dewar's model are grown in isolation, with LL specified as an input. Thus the model remains silent on the conditions that enable a range of LL values to coexist with one another. Nevertheless, their model provides an important advance towards explaining the structure of covariation among leaf traits, including interactions with nutrient supply.

## A strong test of the time-discounting hypothesis

Overall, our results and those of at least one previous study (Selaya & Anten, 2010) suggest time-discounting effects are key to understanding the diversity of LL strategies found in most vegetation types (Scenario 1 in Fig. 1). Theory about LL is founded on the idea that different strategies must have equivalent fitness in order to coexist (Fig. 1); otherwise natural selection would replace inferior strategies with those of higher fitness, through either directional selection or species replacement (Westoby *et al.*, 2000). Under the time-discounting hypothesis, the dynamics of growth and competition play a key role in generating fitness equivalence across species, in place of, or in association with, covariation of LL with other traits and factors (Fig. 1). So species with higher LL are expected to have a greater $R_C$ until time-discounting effects are accounted for.

Although long-LL leaves may yield a greater total return on investment (when discounting effects are excluded), that return is realized over a long timeframe, set by the species' mean LL. By contrast, leaves with short LL yield a higher rate of return per unit time, but for a shorter duration (Westoby *et al.*, 2000; Wright *et al.*, 2004). The time-discount rate takes account of the fact that C returns from leaves received earlier are worth more to the plant because this photosynthate can be reinvested in new leaf area, which also yields a further C return to the plant (Blackman, 1919; Harper, 1989; Westoby *et al.*, 2000). This process of quick return and reinvestment of C – which is directly akin to the effect of receiving compound interest in one's bank account – explains why species with short LL achieve higher growth rates as seedlings and saplings than do those with long LL (Reich *et al.*, 1992).

In principle, one could use the C revenue streams generated by our study to estimate long-term growth rates in leaf area for different species, by applying known techniques for estimating a population's intrinsic rate of increase (De Roos, 2008). This would account for one aspect of the time-discounting effect. However, such calculations may fail to show the desired fitness equivalence, because they would still be based on a static estimate of a species' C revenue stream; and thus fail to account for changes in revenue arising through competition. Over time, fast-growing individuals overtop and shade slower-growing individuals. As long-LL species tend to be slow-growing as seedlings and saplings (Reich *et al.*, 1992), their revenue is expected to decline more sharply when grown in competition with short-LL species. This dynamic, observed in the study of Selaya & Anten (2010),

may be responsible for the differences in light environment detected in our study, with the resultant influences on $R_C$.

While the results of our study provide some support for the time-discounting hypothesis, they are based on estimates of light income spanning a narrow window in the lifespan of an individual. Ultimately, a strong test of the time-discounting hypothesis is needed. To achieve this, it is essential to account for the dynamics of growth through ontogeny and to capture the long-term effects of competition on reproductive success. Similarly, many existing canopy models (McMurtrie & Dewar, 2011) are static, meaning they focus on canopies at equilibrium (Anten & During, 2011). A new generation of trait-, size- and patch-structured ecosystem models, able to capture the influence of traits on growth across the entire life cycle and in the presence of disturbance and competition (Moorcroft *et al.*, 2001; Falster *et al.*, 2011), potentially offer new opportunities to quantify the importance of time-discounting effects and to understand the processes allowing coexistence of short- and long-LL species. Ultimately, a number of paradoxes in the literature may be reconciled through such an approach.

## Conclusion

Results of our study show that, at least for this species mix in Australian woodland, species with longer LL received a greater lifetime return in C fixed per unit C, N and P invested. These results support longstanding hypotheses about the benefits of extended LL (Schulze *et al.*, 1977; Chabot & Hicks, 1982) and suggest a key role for time-discounting effects in equalizing fitness across species. However, examining our results in the context of the findings of other studies, and the limits of all existing studies (including ours), which include small ($\leq$ 12) and idiosyncratic species sets and quantitatively limited physiological estimates, leads us to suggest that we still know surprisingly little about how differences in leaf economic traits translate in terms of resource yields over meaningful hierarchical (e.g. organ, individual), temporal and spatial scales. This may be disappointing, but suggests that the gate remains wide open for future advances in studies of whole-plant C balance and plant C, N and water economies in relation to LL.

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## Supporting Information

Additional supporting information may be found in the online version of this article.

**Notes S1** Average trait values and simulation output for the 10 species studied (the factors included in each simulation are outlined in Table 2).

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