Waiting can be an optimal conservation strategy, even in a crisis discipline

Gwenllian D. Iacona[a,b,c,1], **Hugh P. Possingham**[a,b,c,d], and **Michael Bode**[e]

[a]Australian Research Council Centre of Excellence for Environmental Decisions, The University of Queensland, St Lucia, QLD 4072, Australia; [b]Centre for Biodiversity and Conservation Science, The University of Queensland, St Lucia, QLD 4072, Australia; [c]School of Biological Sciences, The University of Queensland, St Lucia, QLD 4072, Australia; [d]The Nature Conservancy, Arlington, VA 22203-1606; and [e]Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

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Biodiversity conservation projects confront immediate and escalating threats with limited funding. Conservation theory suggests that the best response to the species extinction crisis is to spend money as soon as it becomes available, and this is often an explicit constraint placed on funding. We use a general dynamic model of a conservation landscape to show that this decision to "front-load" project spending can be suboptimal if a delay allows managers to use resources more strategically. Our model demonstrates the existence of temporal efficiencies in conservation management, which parallel the spatial efficiencies identified by systematic conservation planning. The optimal timing of decisions balances the rate of biodiversity decline (e.g., the relaxation of extinction debts, or the progress of climate change) against the rate at which spending appreciates in value (e.g., through interest, learning, or capacity building). We contrast the benefits of acting and waiting in two ecosystems where restoration can mitigate forest bird extinction debts: South Australia's Mount Lofty Ranges and Paraguay's Atlantic Forest. In both cases, conservation outcomes cannot be maximized by front-loading spending, and the optimal solution recommends substantial delays before managers undertake conservation actions. Surprisingly, these delays allow superior conservation benefits to be achieved, in less time than front-loading. Our analyses provide an intuitive and mechanistic rationale for strategic delay, which contrasts with the orthodoxy of front-loaded spending for conservation actions. Our results illustrate the conservation efficiencies that could be achieved if decision makers choose when to spend their limited resources, as opposed to just where to spend them.

systematic conservation planning | extinction debt | conservation finance | dynamic optimization | forest restoration

Irreversible biodiversity loss makes conservation a race against time (1–3). In response to this state of "crisis" (4), conservation projects usually aim to maximize impact by "front-loading," expending their resources on conservation activities as rapidly as possible (5–7). Many studies support this orthodoxy, with specific examples that recommend action as soon as resources become available (8–10). Delays incur opportunity costs, both because biodiversity losses are often irreversible [e.g., species, phylogenetic diversity, or pristine habitat (11, 12)] and because fewer options remain available to managers as time passes [e.g., properties become unavailable (13) or political will disappears (14)]. Although the front-loading of project spending is an understandable response to imminent threats, it may not be the most efficient decision. Finance theory stresses an optimal balance between immediate consumption and capital investment (15), even in the face of accelerating threats. Operations research similarly recognizes that the short-term costs incurred by delay can be offset by superior long-term outcomes (16–18).

Delayed actions improve long-term outcomes if deferment is used to build future capacity—the ability to pursue a desired outcome. Optimal growth theory offers a close ecological analogue to this phenomenon: plants aim to maximize their lifetime reproductive success, but they often achieve this by completely deferring any investment in reproductive activities [e.g., flowers or seeds (19)]. Fitness is instead maximized by early investments that increase an organism's capacity to act (e.g., its photosynthetic system) or that allow it to store resources (e.g., root stock) while waiting for a period of lower competition (20). Delays can confer similar benefits on conservation actions via comparable mechanisms, including earning interest, learning, or building capital. Economic interest offers the most conceptually straightforward example: an increase in principal can be obtained by temporarily lending funds to other sectors of the economy. Learning through monitoring (21–23) and research (24, 25) delays actions but offers an opportunity to improve the efficiency of those actions when they are eventually taken. Finally, investments in technology, human capital, or infrastructure can also increase the efficiency of future spending (26).

Regardless of the mechanism, delays are only optimal when their benefits outweigh the concurrent increase in threats. In conservation, the optimal timing is determined by a competition between two rates: the rate of decline of conservation assets and the rate at which capacity increases. These rates operate in different directions and also have different characteristics. The decline of conservation assets can follow complex trajectories: the simultaneous accumulation and relaxation of extinction debts (27); the slow–fast–slow dynamics of regional habitat loss (28); or critical threshold dynamics found in nonlinear ecological and climate systems (29, 30). Conservation capacity in the simplest sense could be money in a bank, which can exponentially increase over time due to compound interest but is subject to economic shocks and reversals (14, 31). Learning generally improves conservation outcomes, but at a diminishing marginal rate (21). Conservation dynamics are therefore temporally heterogeneous, and this creates periods of time during which actions will

Significance

Every year, more species are driven to extinction by the combined pressures of habitat destruction, invasive species, and climate change. These ongoing losses have created a "crisis culture" in conservation, where project funds are spent as soon as they are received. We challenge this orthodoxy and demonstrate how strategic delays can improve efficiency. Waiting can allow agencies to leverage additional benefits from their funds, through investment, capacity building, or monitoring and research. With the right amount of delay, limited conservation resources can protect more species. Surprisingly, they can even do so in less time. Our results suggest that, in addition to their current focus on where to target resources, conservation managers should carefully choose when to spend these funds.

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[1] To whom correspondence should be addressed. Email: g.iacona@uq.edu.au.

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be more effective. Systematic conservation planning improves outcomes by identifying the most efficient locations to act in space. In a direct analogy, a systematic approach is needed to identify the most efficient points in time to undertake actions.

In this paper, we formally model the general trade-off between the benefits of waiting and the costs of delay. We consider this trade-off in the context of an extensively studied conservation management problem, species extinction driven by habitat loss (32). We parameterize the model for two case studies—the Mount Lofty Ranges in Australia and the Atlantic Forests in Paraguay—where widespread clearing has created an extinction debt that can only be addressed through habitat restoration. In these examples, managers can defer spending to accrue financial interest, but species will continue to be lost during this delay as the extinction debt relaxes (33, 34).

Dynamic Habitat Model

We model the impacts of conservation projects in a landscape using a system of deterministic differential equations that link conservation actions through time with a biodiversity conservation goal. The model captures the essential dynamics of restoration and extinction debts in degraded landscapes, but does not include factors (e.g., stochasticity, spatial heterogeneity) which will have limited influence on the optimal timing but which preclude closed-form solutions. Its structural simplicity therefore emphasizes the contrast between waiting and spending.

At any given time, habitat is either not supporting species because it is cleared $C(t)$, or is intact $R(t)=1-C(t)$ and can support species $[0\le C(t), R(t)\le 1]$. Managers are given a single endowment of funds, $B(t=0)=B_0$, which they can spend at any time to convert cleared habitat into intact habitat by restoration, at a cost c_R per unit area. Unspent funds are invested and accrue interest at proportional rate r. In the analyses that follow, we use inflation-adjusted interest rates, which allow us to use a constant value for c_R. Managers define a proportional spending schedule $0\le u(t)\le 1$, with the objective of minimizing the number of extinctions. These dynamics are described mathematically using two habitat equations and a budget equation:

$$\frac{dR}{dt}=\frac{u(t)B(t)}{c_R}, \qquad \textbf{[1a]}$$

$$\frac{dC}{dt}=-\frac{u(t)B(t)}{c_R}, \qquad \textbf{[1b]}$$

$$\frac{dB}{dt}=(r-u(t))B(t). \qquad \textbf{[1c]}$$

We assume that the species–area relationship (SAR) allows equilibrium species richness to be predicted based on the area of intact habitat:

$$S^{*}=\alpha R(t)^{z}, \qquad \textbf{[2]}$$

where α represents regional species richness and z denotes the species accumulation rate in the region. Historic species richness is represented by $S^{*}=\alpha$ when $R=1$ and all of the habitat is intact. If the amount of current intact habitat is insufficient to support the current number of extant species [i.e., if $S(t)>S^{*}$], an extinction debt exists and species will be lost as this debt relaxes at proportional rate θ:

$$\frac{dS(t)}{dt}=-\theta[S(t)-S^{*}]=-\theta[S(t)-\alpha R(t)^{z}]. \qquad \textbf{[3]}$$

The managers' objective is to identify the spending schedule that maximizes the number of extant species at some future time T:

$$\max_{0\le u(t)\le 1} S(T). \qquad \textbf{[4]}$$

Analytic Solution for Optimal Single Disbursement. The simplest formulation of our problem begins with no intact habitat [$R(0)=0$], but with a large extinction debt (i.e., all species remain extant: $S_0=\alpha$). A manager delays spending for t_S years, and then spends all of the accumulated funds in a "single disbursement," allowing the restoration of area $R(t_s)=B(t_s)/c_R$. The optimal disbursement time maximizes the number of protected species, defined as follows:

$$S_p=\max_{0\le t_s\le T}[\min\{\alpha R(t_s)^{z}; S(t_s)\}], \qquad \textbf{[5]}$$

The first term in the set applies when the number of species extant at t_s equals or exceeds the number that can be supported by the restored land. The second term applies when the extinction debt has relaxed to below the level that can be supported by the restored land (i.e., the managers waited too long). Since the increase in the first term and the decrease in the second term are both monotonic, the optimal time to disburse the funds occurs when the functions intersect (Fig. 1). For $r>0$, this occurs at time:

$$t_s^{*}=z\frac{\ln\left(\frac{c_R}{B_0}\right)}{rz+\theta}. \qquad \textbf{[6]}$$

This solution shows that, for a single disbursement, some length of delay is always optimal, given two common conservation conditions. First, the initial budget must be insufficient to immediately eliminate the extinction debt. This condition is ubiquitous in conservation (35, 36). Second, inflation-adjusted real interest rates must be positive. This condition is almost always true, even for conservative instruments such as Treasury bonds (Fig. S1). The optimal length of the delay is determined by the initial restoration budget, and the rates of change within the system (see *SI Model of the System Dynamics* for details). The numerator shows that expensive restoration costs (relative to the budget: c_R/B_0) will encourage longer delays, while the denominator indicates that faster extinction debt relaxation (θ) and higher interest rates (r) incentivize front-loading. Higher interest rates make investment more attractive because capacity to act increases more rapidly. Higher interest rates therefore result in shorter delays because it takes less time to amass the resources required to fund all necessary restoration activities (Fig. 1).

Optimal Disbursement Schedule. The single disbursement solution reveals the essential factors that govern the duration of the optimal delay, but conservation resources are often obtained and expended over a longer period. In the following two case studies, we identify a disbursement schedule that maximizes bird species richness at the end of the planning horizon. We use each case study to illustrate a different project funding scenario: the Mount Lofty Ranges case study receives a recurrent annual budget from a central funding organization; the Atlantic Forests case study is structured as a "sinking fund," where an initial lump sum is raised to fund a single initiative, without an expectation of ongoing funds (37). In both cases, the managers can choose to spend a proportion of their resources every year and accrue interest on the remainder. Operationally, we used numerical optimization (Matlab R2016a; MathWorks) to identify the disbursement schedule $u(t)$ that maximizes Eq. **4** under the constraints of Eqs. **1**–**3**. See *SI Model of the System Dynamics* for further details.

Case Study 1: Mount Lofty Ranges (Australia). The Mount Lofty Ranges woodlands ecoregion (MLR) in Southern Australia acts as a habitat island for woodland bird species because it

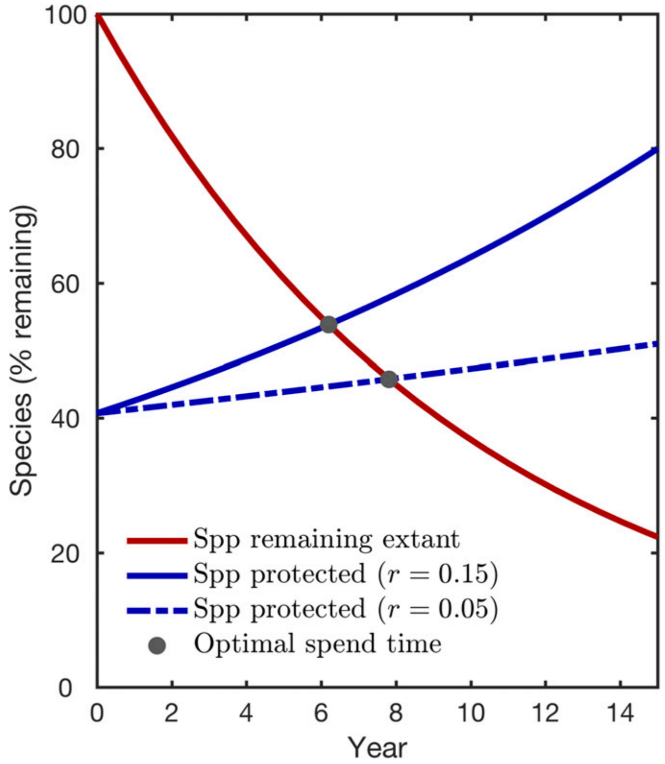

Fig. 1. The optimal delay is determined by the intersection of two curves, each defined by a critical system rate. The red line shows the number of species remaining extant if funds are not spent. The extinction debt relaxation rate θ defines the downward slope of this curve. The blue lines show the number of species that could be protected if accumulated funding were disbursed at a given point in time. The upward slope of these two curves reflects an increase in resources via the financial interest rate r, shown for two different values. To generate this figure, $z = 0.3$, $\alpha = 1$, $B_0 = 1$, $c_R = 20$, and $0 \leq R(t) \leq 1$.

experiences substantially higher rainfall (400–1,100 mm/y) than surrounding ecosystems. Historically, 115 species of birds were found in this ≈500,000-ha region. Extensive land clearing has reduced the forest cover by 87% (38) (Table S1), and the SAR predicts that this amount of habitat loss will eventually cause 35 bird extinctions (39). At present, only eight extinctions have occurred, with a further eight species considered near extinction (40) (Table S2); this indicates the presence of a sizeable extinction debt (39). Biogeographic analyses of southern Australian forest bird communities estimate the relevant SAR parameters to be $z = 0.17$ and $\alpha = 13.6$ (39), and historical survey data and forest cover records indicate an extinction debt relaxation rate of $\theta = 2.5 \times 10^{-3}\ \mathrm{y}^{-1}$. Restoration costs ($c_R$) are estimated at $1,132 (2016 AUD per hectare). We assume that decision makers can secure a constant 5.8% interest rate, based on Australia's inflation-adjusted lending interest rate over the past 25 years (41). Revegetation has been shown to counteract further bird decline in the MLR (42, 43), and at least $500,000 (2016 AUD) per year is spent protecting and restoring priority areas within the ecoregion. See *SI Model of the System Dynamics* and Fig. S2 for an explanation of these parameters.

Fig. 2 shows that, if this level of annual funding is continually and immediately invested into direct restoration of habitats, the existing extinction debt will be negated in 250 years. Such front-loading of the disbursement of funds will conserve 102 species by restoring 116,400 ha of habitat. In contrast, if managers are allowed to delay spending, this extinction debt could be negated within 78 years, with 147,300 ha of habitat restored. The optimal solution invests the annual budget for more than 40 years before undertaking direct conservation actions, with the accumulated funds gradually liquidated over the subsequent three decades. During the initial phase of delay, more extinctions occur than in the front-loaded schedule (Fig. 2). However, the optimal spending schedule eventually reduces the number of extinctions by 51% over business as usual and allows the extinction debt to be eliminated within 78 years. A delay therefore allows managers to achieve their aims in less than half the time.

Our optimization approach allows the optimal solution to take the form of a single disbursement, but the best decision is to gradually spend the invested funds over a series of years (Fig. 2). A small amount of early spending slows down the species loss rate (Eq. **3**), allowing managers more time to invest the remaining resources, and therefore to protect more species (see *SI Model of the System Dynamics* and Fig. S3). A sensitivity test with a more conservative interest rate estimate, based on Australian Treasury bond returns, resulted in a longer optimal delay (*SI Model of the System Dynamics* and Fig. S4). However, we note that our results do not represent a strict recommendation to wait decades before acting, since a delay of this length would be untenable for most conservation organizations. Instead, the optimal solution emphasizes the potential efficiencies that are foregone by a decision to front-loading spending.

Case Study 2: Atlantic Forest (Paraguay). South America's Atlantic Forest is a consensus global conservation priority (32). There is evidence for a substantial extinction debt in the ecoregion (33), with dramatic clearing in the 1980s leaving little intact habitat (≈25%) and many threatened species, but causing few immediate extinctions. International and national initiatives (e.g., Pacto Mata Atlantica, The Nature Conservancy's One Billion Trees program, World Wildlife Fund, Paraguay Biodiversidad) aim to restore forest before any of the 124 forest-dependent endemic bird species go extinct (33).

Habitat dynamics for the region are parameterized using $\theta = 0.03\ \mathrm{y}^{-1}$ (44), $z = 0.18$, and $\alpha = 16$ (45), and restoration costs are estimated at $153,000 km^{-2} (46) (2016 USD). All resources made available to the project are placed into a "sinking fund" in the first year of the project (37), and we assume an initial investment equivalent to Brazil's FUNBIO fund of $500 million (2016 USD). While invested, the sinking fund returns a rate of 3.6% per year, based on the US lending interest rate adjusted for inflation over the past 25 years (41). See *SI Model of the System Dynamics* for an explanation of these parameters.

Fig. 3 shows that, if spending is heavily front-loaded (specifically, entirely within the first 5 years), species loss will halt in 143 years, protecting 87 species with 3,340 km^2 of additional restored habitat. Alternatively, in the optimal delayed schedule, managers accrue interest on their unspent funds for 40 years before they start to disburse them. When the accumulated funds are spent over the following nearly 20 years, the restored habitat will protect 96 species, restoring 12,000 km^2 of forest habitat in the process, and halting extinction within 58 years. Once again, an optimal delay accelerated conservation outcomes and achieved a 23% reduction in expected extinctions. A larger initial budget or higher interest rate will result in a shorter delay (including a small amount of spending in the first year) but front-loading remains suboptimal (*SI Model of the System Dynamics* and Fig. S5). More conservative interest rate estimates, based on Federal Reserve bond returns, result in a longer optimal delay (*SI Model of the System Dynamics* and Fig. S6).

Discussion

Our results emphasize an important additional dimension in systematic conservation planning by demonstrating that there are optimal times to take action, in addition to optimal locations. When conservation capacity can increase faster than the irreversible rate of biodiversity decline, a delay of finite duration allows projects to

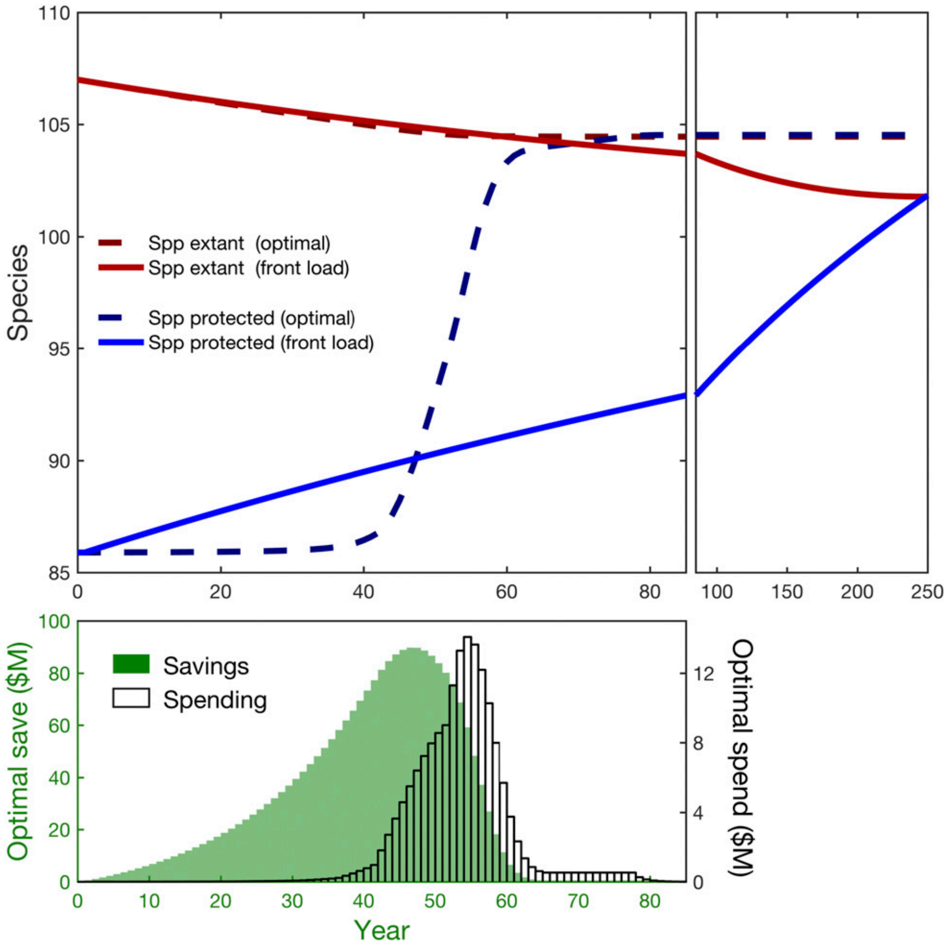

Fig. 2. Optimal schedule for the Mount Lofty Ranges, Australia, case study. *Top* shows extant (red lines) and protected (blue lines) species under the optimal (dashed lines) and front-loading strategy (solid lines). The distance between the blue and red lines reflects the size of the extinction debt. Note the different timescales of the plots. *Bottom* shows the amount of funding available to the manager over time (green), and the amount spent (bars) in yearly increments under the optimal strategy.

leverage additional advantage from conservation funds. Strategic delay can thus allow decision makers to protect more species—even to complete projects more rapidly—suggesting that front-loaded conservation projects may be overlooking a substantial source of efficiency in the temporal dimension. The optimal amount of delay will balance the rate of biodiversity loss with the rate at which waiting increases managers' capacity to act. In our specific examples, we use financial interest to represent the benefits of waiting because it is conceptually simple, and extinction debts to represent the incentive to act immediately because they offer a well-understood link between the loss of habitat and the loss of species. However, competing rates of biodiversity loss and capacity accumulation are, in some form, present in all conservation problems.

Our central conclusion is that a focus on future capacity, at the expense of immediate action, can deliver superior outcomes over relevant timescales. Many conservation organizations clearly understand this concept and focus on activities that deliver delayed, long-term benefits (47). Prominent examples include environmental education and awareness initiatives, climate change adaptation projects, and conservation policy think tanks. However, our work demonstrates that delayed action can also deliver efficiencies at the scale of individual projects, which are primarily concerned with direct conservation actions such as restoration. This conclusion runs counter to standard conservation practice at a project level: many sources of one-off funding (e.g., grants, offsets) ask projects to deliver and report on outcomes within short time frames. Similarly, philanthropic rating schemes tend to encourage organizations to spend more of their income immediately, on direct actions (48, 49). Just as spatially constrained conservation planning cannot deliver the best outcomes (50, 51), temporal constraints incur opportunity costs, by restricting managers' freedom to act at the most effective point in time.

Previous conservation theory has shown how prioritizing actions across time can result in superior outcomes (e.g., refs. 52–57). However, these dynamic optimizations still treat conservation as a race against time—they essentially identify where to front-load spending. In contrast, we take advantage of variation along the temporal dimension to identify efficient periods of time in which to act. An assessment of the shadow values of alternative actions confirms the existence of periods of high relative efficiency (Fig. S7).

Our ideas also have close analogues in environmental and resource economics, but with important differences. Real options analysis has long understood that delaying irreversible actions can be an optimal strategy, because waiting allows decision makers to learn more about the situation, and to respond better to uncertain future events (58–60). Our results provide a parallel justification for waiting, but where the returns to management actions are known with certainty because the system dynamics are deterministic. Our conclusions are closely related to Hotelling's rule, which states that nonrenewable resources should initially be strategically underexploited to increase

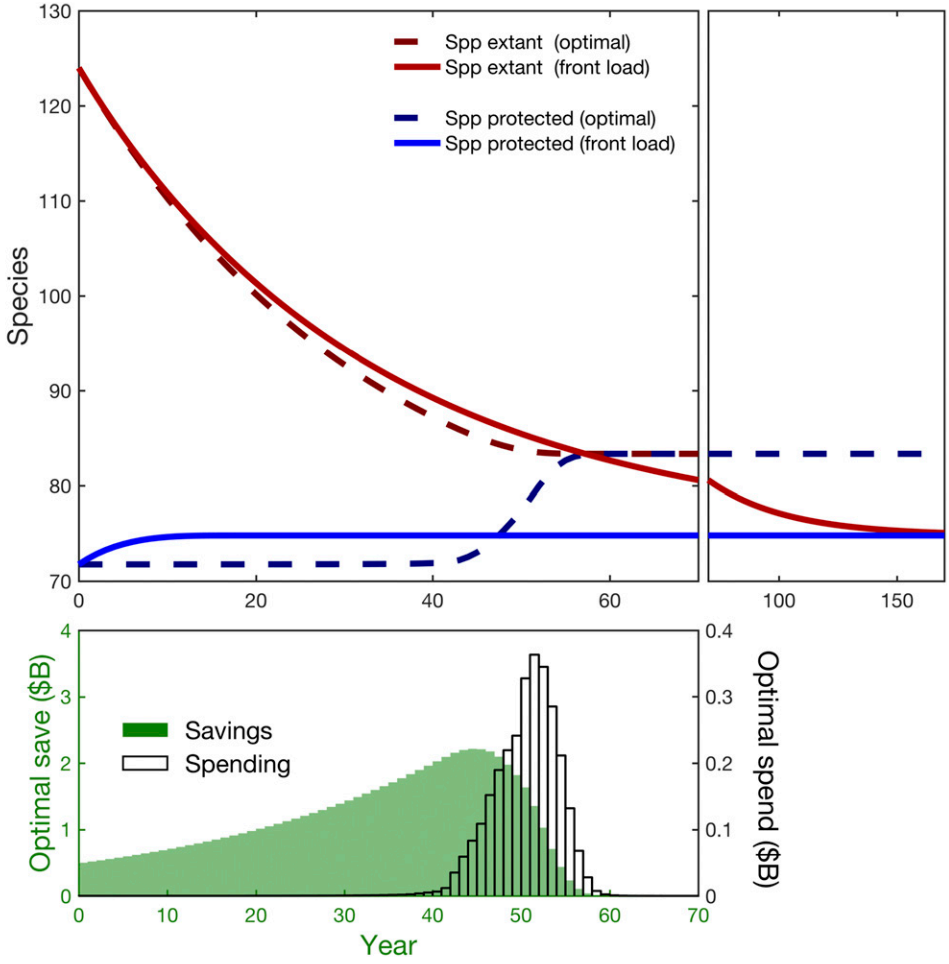

Fig. 3. Optimal schedule for the Atlantic Forest, Paraguay, case study. *Top* shows extant (red lines) and protected (blue lines) species under the optimal (dashed lines) and front-loading strategy (solid lines). The distance between the blue and red lines reflects the size of the extinction debt. Note the different timescales of the plots. *Bottom* shows the amount of funding available to the manager over time (green), and the amount spent (bars) in yearly increments under the optimal strategy.

future revenue (61). Similarly, Fisher's rule illustrates how the timing of logging in production forests should reflect the timber growth rate, price, and economic discount rate (62). However, the conservation problem is the inverse of these resource extraction problems. Rather than maximizing the revenue generated by exploiting a limited resource, we seek to minimize the loss of a declining resource, while operating under tight budget constraints. The result is that the discount rate works against resource managers and for conservation managers (because it acts to increase their capacity). Nevertheless, because they are pursuing opposite goals, in both cases lower interest rates encourage longer strategic delays.

We made a series of simplifying assumptions to clearly highlight the competing rates that drive the optimal delays. Our ecological and economic models are deterministic, whereas both systems experience variability and shocks. Thus, both the costs (e.g., land prices) and benefits of delay will become more uncertain in more distant futures. These sources of uncertainty will change our model recommendations and are a critical reason why our results—particularly those that recommend decades of delay—should not be used prescriptively. However, these factors do not change the central conclusion, that strategic delay can deliver conservation benefits. Ecologically, our models assume that restoration rapidly and predictably restores habitat, but functional habitat can lag restoration actions by many decades, and restored habitat may never be fully equivalent (63). However, more complex alternative models that include time lags and uncertainty in restoration do not affect conclusions in comparable models (34).

The ability of conservation organizations to capitalize on temporal opportunities will be subject to constraints on institutions' financial flexibility. The benefits of investment for future spending will be unavailable to agencies that operate under short budget cycles, and penalize surpluses (64), or to funding instruments (e.g., grants) that expect spending to occur within defined time frames. Our results suggest that there is an advantage to developing conservation institutions and instruments that are free of these constraints. For instance, a growing number of organizations are establishing long-term conservation trust funds (65, 66) [e.g., The Nature Conservancy's Land Preservation Fund (67)] or are using investments to secure perpetual management income (e.g., Tasmanian Land Conservancy Management Endowment). Sinking funds, which we modeled in our Atlantic Forest case study (Fig. 3), are another vehicle for leveraging interest from conservation resources and for avoiding front-loaded spending. These funds are becoming increasingly common [e.g., EcoFundo in Ecuador, or FUNBIO in Brazil (68)] and are well-suited to one-off funding sources such as large endowments or offsets. Our results highlight the importance of the temporal flexibility offered by these financial instruments but emphasize how their disbursement time frames should reflect the ecological dynamics of the target ecosystems.

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