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Abstract: Phenology has achieved a prominent position in current scenarios of global change research given its role in monitoring and predicting the timing of recurrent life cycle events. However, the implications of phenology to environmental conservation and management remain poorly explored. Here, we present the first explicit appraisal of how phenology — a multidisciplinary science encompassing biometeorology, ecology, and evolutionary biology — can make a key contribution to contemporary conservation biology. We focus on shifts in plant phenology induced by global change, their impacts on species diversity and plant-animal interactions in the tropics, and how conservation efforts could be enhanced in relation to plant resource organization. We identify the effects of phenological changes and mismatches in the maintenance and conservation of mutualistic interactions, and examine how phenological research can contribute to evaluate, manage and mitigate the consequences of land-use change and other natural and anthropogenic disturbances, such as fire, exotic and invasive species. We also identify cutting-edge tools that can improve the spatial and temporal coverage of phenological monitoring, from satellites to drones and digital cameras. We highlight the role of historical information in recovering long-term phenological time series, and track climate-related shifts in tropical systems. Finally, we propose a set of measures to boost the contribution of phenology to conservation science. We advocate the inclusion of phenology into predictive models integrating evolutionary history to identify species groups that are either resilient or sensitive to future climate-change scenarios, and understand how phenological mismatches can affect community dynamics, ecosystem services, and conservation over time.

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Americas (Zoological) Editor

Biological Conservation

Response to Reviewers

Ms. Ref. No.: BIOC-D-15-00602R1

Title: Linking plant phenology to conservation biology

Biological Conservation

Dear Dr Galetti ,

We hereby submit the revised draft of our 'Perspectives' manuscript entitled "Linking plant phenology to conservation biology" to which we now incorporate the rather minor changes suggested by the reviewers. While responding to those very positive comments, we also indicate how we have incorporated the reviewers' remarks.

We thank you and the reviewers again for all the suggestions that have improved our manuscript.

Best regards,

Patrícia Morellato

Reviewers' comments:

Reviewer #3: BIOLOGICAL CONSERVATION- BIOC-D-15-00602R1

This is a timing review on phenology studies, an issue that has become topical in recent years because its relevance to understand population responses to global change. Certainly, an increasing number of ecological studies show the importance of a fine characterization of the phenophases of a plant community to understand their functioning and predict their functional responses to different triggers of global change.

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The MS is well written, integrates interesting different aspects of plant phenology and provide a guide to include phenology in prospective long-term studies and management plans. Therefore the study is of general interest for a wide audience, particularly for Biological Conservation readers.

Next, I suggest some changes to improve the current version of the MS

1. Authors comment the effect of climate and land use change on Section 4. For example, they argue that edge effect "increase of flowering and fruiting activity" (Line #389) or fragmentation affect reproductive success. Yet, these are functional responses of plant populations to different types of disturbances/changes, but they do not necessary entail changes in phenology. Please, review the MS and make sure that you only include examples that make the case for phenological shifts in response to climate and land use changes.

Response: *Thanks for the comment. We completely understand the reviewer's concern, but we have long used a broader conceptual definition of phenological changes which should not only represent shifts in the timing of reproduction but also shifts on the intensity (amplitude) and duration of plant phenophases. Therefore, increases in flowering and fruiting activity can indeed be considered phenological responses to a given environmental cue. In the paper we refer to elevated levels in reproductive effort (i.e. more frequent, longer, or more intensive flowering and fruiting activity) in plants within edge-dominated habitats. These in our view are 'real' resource allocation shifts within the metabolic pathway alternatives available to plants, so we see them as true phenological responses. We agree that the effect on plant reproductive success is a functional response that is a consequence of a phenological shift, as reported in the text. We further reviewed and double-checked the text to make sure we only include examples of phenological shifts in response to climate change and land use change as suggested.*

2. Section 3.2 Flowering and pollinators could some recent findings that correlated fragmentation with pollinator movement patterns and fecundity levels in forest species (Breed et al. 2012; Breed, Christmas & Lowe 2014)

Response: *We thank you for the suggestion and we have added one of the suggested references (Breed et al. 2012).*

3. There are some weird expressions: "the fabric of interactions and competitive relationships" (Line#345)

Response: *We do not see this as "weird", but may be too poetic. We have therefore rephrased the text to: "the organization of interactions and competitive relationships"*

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4. Besides environmental changes such as temperature, phenology also responds to invariant clues, such as photoperiod. Please, comment the effect of these opposes forces.

Response*: We include a sentence regarding the importance of photoperiod as an invariant clue to define the timing and periodicity of plant phenology of tropical environments with low* climatic seasonality (Lines#135 to 141).

5. There are interesting concepts along the MS that should be presented in the introduction. The introduction section should include a brief overview about phenospecies or the idea of including phenology as a functional trait, or about niche changes.

Response*: Thank you for the suggestion. We have therefore incorporated into the introduction the additional concepts pointed out by the reviewer and removed any repetition from the main text.*

Reference included:

Breed, M.F., Gardner, M.G., Ottewell, K.M., Navarro, C.M. & Lowe, A.J. (2012) Shifts in reproductive assurance strategies and inbreeding costs associated with habitat fragmentation in Central American mahogany. Ecology Letters, 15, 444-452.

*Highlights (for review)

Highlights

- We establish phenology as key research endeavor in applied ecology and conservation
- We show climate-change phenological mismatches affect conservation of mutualisms
- Phenology supports managing impacts such as fire, invasive species or fragmentation
- New technologies improve spatial and temporal coverage of phenology monitoring
- The relevance of phenology as a tool for conservation education and citizen science

Perspectives

Linking plant phenology to conservation biology

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Short title: Phenology and conservation

ABSTRACT

Phenology has achieved a prominent position in current scenarios of global change research given its role in monitoring and predicting the timing of recurrent life cycle events. However, the implications of phenology to environmental conservation and management remain poorly explored. Here, we present the first explicit appraisal of how phenology — a multidisciplinary science encompassing biometeorology, ecology, and evolutionary biology — can make a key contribution to contemporary conservation biology. We focus on shifts in plant phenology induced by global change, their impacts on species diversity and plant-animal interactions in the tropics, and how conservation efforts could be enhanced in relation to plant resource organization. We identify the effects of phenological changes and mismatches in the maintenance and conservation of mutualistic interactions, and examine how phenological research can contribute to evaluate, manage and mitigate the consequences of land-use change and other natural and anthropogenic disturbances, such as fire, exotic and invasive species. We also identify cutting-edge tools that can improve the spatial and temporal coverage of phenological monitoring, from satellites to drones and digital cameras. We highlight the role of historical information in recovering long-term phenological time series, and track climate-related shifts in tropical systems. Finally, we propose a set of measures to boost the contribution of phenology to conservation science. We advocate the inclusion of phenology into predictive models integrating evolutionary history to identify species groups that are either resilient or sensitive to future climate-change scenarios, and understand how phenological mismatches can affect community dynamics, ecosystem services, and conservation over time.

Keywords: plant-animal interactions; restoration ecology; climate change; monitoring; management; resource availability

1. INTRODUCTION

Phenology is an integrative environmental science that has achieved a prominent position in current global-change research, due to its capacity to monitor, understand and predict the timing of recurrent biological events related to climate, such as bird migration, frog calling, and leafing, flowering and fruiting of plant populations (Rosenzweig et al. 2008). Phenological studies also provide key knowledge that can be incorporated into predictive models forecasting climate change scenarios (IPCC 2014; Rosemartin et al. 2014).

Climate is the main factor controlling and regulating phenological events in plants, and global warming has affected species distributions and the timing of leaf change and reproduction (Chuine and Beaubien 2001; Menzel et al. 2006), with likely effects on biogeochemical processes and physical properties of the atmosphere (van der Sleen et al. 2015). Across the tropics, subtle changes in temperature have been regarded as a less important phenological trigger, whereas seasonal variation in rainfall has been usually considered as an environmental cue for phenology (Borchert 1998; Morellato et al. 2013; Morellato et al. 2000). However, plant phenology responses to invariant cues, such as photoperiod, may be important in defining the timing, periodicity and particularly the synchrony of plant reproduction, especially in tropical environments where climatic seasonality is low (Borchert et al. 2005; Rivera and Borchert 2001). Long-term phenological time series from the Northern Hemisphere have shown a strong link between the earlier onset of leafing and flowering and elevated temperatures due to climate change (Menzel et al. 2006; Schwartz et al. 2006). However, information on the effects of climate change in tropical regions is still sparse, particularly in the Southern Hemisphere, and long-term data sets are rare (Chambers et al. 2013; Morellato et al. 2013).

The management and conservation of natural systems can be critically enhanced with a greater understanding of the triggers regulating and controlling plant cycles and differences across species, populations and communities (Miller-Rushing and Weltzin 2009; Polgar and Primack 2011). In this regard, recent improvements in vegetation monitoring techniques such as repeated digital photographs, and the growing field of satellite-derived phenology (Alberton et al. 2014; Morisette et al. 2009; Richardson et al. 2013) have paved the way to inferences about temporal shifts at multiple scales that can be applied worldwide.

Despite the well-known connection between phenology and climate change (IPCC 2014), its relevance and implications for resource conservation and management remain poorly understood. These implications include the synchronicity between flowering and pollinator activity or fruiting and seed disperser activity, the connectivity and gene flow through pollen and seed movements across fragmented landscapes, and the forecasting of climate-change effects on species distributions and ecosystem processes. In fact, plant phenology links different hierarchical levels and functional groups within a community, including decomposers, detritivores, herbivores, predators, pollinators, and seed dispersers. Consequently, efforts to conserve these temporal links will safeguard the functionalities and long-term maintenance of ecosystem services. In this context, we explore how phenology — as a multidisciplinary science encompassing biometeorology, ecology, and evolutionary biology (Wolkovich et al. 2014) — can be harnessed as a key research endeavour in applied ecology and conservation biology, with special emphasis on the tropics.

Our framework is centered on the potential shifts in plant phenology driven by global environmental change and their impact on the high diversity of species and plant-animal interactions found in the tropics (Figure 1). One key issue would be to incorporate phenology into community-level coexistence theory tied to the species niche concept. As such, broadening the ecological niche to a more explicit temporal space would allow investigators to test hypotheses and make predictions regarding plant responses to environmental and competitive changes at different scales (e.g. Schellhorn et al. 2015; Wolkovich and Cleland 2011; Wolkovich et al. 2014). We highlight issues where phenology can provide a major contribution to conservation science. We begin addressing how phenology can help conservation efforts in relation to plant-animal interactions from the perspective of resource availability in plant populations and communities, and bottom-up trophic organization. We point out the relevance of ecological networks to understand the effects of temporal changes and mismatches between resources and consumers on the maintenance of mutualistic interactions (Figure 1). We examine how phenological mismatches affect communities, ecosystem services, and ecosystem recovery dynamics over time. Furthermore, we discuss how knowledge of plant phenology can help evaluate and mitigate the effects of land-use change on ecological interactions, including habitat fragmentation, edge effects, and fire. We also consider the thorny problem of exotic and invasive species and the key role of phenology in managing biological invasions and restoring natural ecosystem integrity. We indicate the use of phenology as a functional trait that, combined with traditional leaf morphology and other traits, would be a more accurate indicator of plant functions related to responses to climate and other environmental cues, such as wildfires (Carvalho and Batalha 2013) or biological invasions (Wolkovich and Cleland 2011).

To our knowledge, this is the first appraisal specifically addressing the implications of phenological knowledge to conservation biology. We propose, therefore, a set of avenues that would allow a stronger and more effective contribution of organismal phenology to conservation science. We point out the value of novel monitoring strategies improving spatial and temporal coverage of phenological monitoring, from satellites to drones and digital cameras. We highlight the key role of retrieving historical information from herbaria and observational studies to fill the gaps of long-term time series (e.g. Hart et al. 2014; Primack et al. 2004; Primack 2014) and shed light on the potential effects of climate change and the consequences of directional phenological shifts in tropical systems. In this sense, the concept of "phenospecies" (i.e. sympatric species that share the same phenological triggers and strategies (Proença et al. 2012), may help reconstruct longer temporal series which can be investigated for biases in reproductive schedules over time. Along this line, advances in dendrochronology may also open new directions for tropical forest conservation from the point of view of past chronological reconstruction, carbon stock accumulation, and ecosystem processes (Schöngart et al. 2011). We propose integrating phenology and species evolutionary history into predictive models, to distinguish between species groups that are either resilient or sensitive to projected climate changes scenarios (Staggemeier et al. 2015; Willis et al. 2008). Finally, we draw attention to the value of citizen science to build phenology databases for conservation (Rosemartin et al. 2014; Theobald et al. 2015) and its unexplored potential in the tropics.

2. METHODS

The present appraisal focuses on phenology from an ecological and evolutionary point of view, its relevance for climate change research and its implications and applications in conservation science, with special attention to the tropics. Our intended audience are conservation practitioners and researchers on phenology and related fields, and we strived to attain a broad but concise perspective of phenology within conservation practices. This appraisal is derived from a two-day workshop on phenology and conservation held by the Phenology Laboratory (UNESP, Brazil) in December 2014.

We discussed a wide range of links between phenology to conservation science, and selected key topics with relevant contributions for the conservation and management of natural systems: phenology and conservation of biotic interactions; phenology, climate and land use change; phenology, evolutionary history and species distributions; data sets and monitoring systems; a set of practical and innovative research approaches; and new avenues for future research. The synopsis was also based on recently published (Hagen et al, 2012, Morellato et al. 2013, Chambers et al. 2013) and ongoing reviews (Buisson et al. 2015, under review; Mendoza et al. 2014; Morellato et al. 2014) conducted by members and collaborators of the UNESP Phenology Lab, and the authors' own experience in phenology and conservation science. The criteria for the systematic literature search are available in Chambers *et al.* (2013) and Morellato *et al.* (2013). We updated these surveys by searching the top conservation science journals using the terms "phenolog*" and "conservation" over the last 10 years. Our goal was to identify relevant research and applications for conservationists and managers, rather than perform an exhaustive review of the topic.

3. PHENOLOGY AND THE CONSERVATION OF BIOTIC INTERACTIONS

3.1. Leafing and herbivory

Studies of leafing phenology have twofold implications for conservation. First, leaf phenology is directly linked to ecosystem processes (Polgar and Primack 2011). Leaf flushing and senescence are related to plant growth, and as such are crucial for understanding plant-water relations and primary productivity in terrestrial ecosystems, as well as gas exchange rates, biogeochemical cycling, and the dynamics of carbon sequestration (Morisette et al. 2009; Polgar and Primack 2011). Investigating the timing and drivers of leaf production and senescence is important to define the length of growing seasons and seasonal patterns of photosynthesis at local to global scales (Morisette et al. 2009). Leaf phenology thus provides key information for ecosystem process models that forecast responses to land-use change, atmospheric chemistry, and climate (Morisette et al. 2009). Thus, shifts at both the onset and end of growing seasons due to climate change may have consequences on ecosystems processes such as net primary production. For instance, increases in temperature and drought frequency may lead to premature leaf senescence in deciduous forests, affecting the efficiency of nutrient resorption and the length of growing seasons, impacting carbon uptake and ecosystem nutrient cycling (Estiarte & Peñuelas 2015), and therefore management practices (e.g. Eriksson et al. 2015).

Second, the timing of leaf production has consequences for interactions between plants and herbivores (Figure 1B), which in the tropics comprise mainly phytophagous insects (Novotny et al. 2006). The conservation of insect populations can be severely affected by changes in the timing of leaf production (Kocsis and Hufnagel 2011), particularly in the context of declining invertebrate faunas, estimated at a global scale to have exceeded 45% between 1970 and 2010 (Dirzo et al. 2014). In turn, shifts in herbivorous insect phenology due to climate change, land-use change, or use of insecticides can threaten plant population viability, leading to increases in herbivore damage (van Asch and Visser 2007).

Plants can adopt several phenological strategies to avoid insect damage, such as synchronizing the timing of leafing peaks to the season with the lowest insect densities, or producing large, synchronous pulses of leaves to satiate herbivores (Aide 1988; Lamarre et al. 2014). Future climatic scenarios may induce higher overlap between insects and plants activity (Fig. 1B), such as prolonged dry seasons delaying leaf production in plants that are stimulated by the first rains, increasing herbivore damage (Aide 1992). Conversely, changes in abiotic factors can also reduce leafing synchrony, which would fail to satiate insect herbivores. Such extreme changes can lead to pest outbreaks and massive losses in plant production (van Asch and Visser 2007).

Phenological mismatches between agricultural pest insects and their natural enemies due to climate change could also decrease the effectiveness of biocontrol measures (Thomson et al. 2010).

Potential trophic mismatches may also arise between vertebrates and plant growing seasons, for instance as documented for caribou in Greenland where a reduction in the spatial variation in plant phenology caused by climate warming decreased offspring production (Post et al. 2008), with implications for managers and conservationists. A detailed knowledge of phenological dynamics of folivorous animals and their host/target plants can therefore be instrumental in the conservation and management of both herbivores and plant populations, and when designing pest control programs in natural and agricultural ecosystems (Baumgartner and Hartmann 2000; Eriksson et al. 2015).

3.2. Flowering and pollinators

The clearly delimited flowering seasonality during springtime, typical of temperate and boreal ecosystems, is generally absent in the tropics. Instead, open flowers are available throughout the year, albeit with varying abundances, inducing periods of peaks and troughs depending on community characteristics, and leading to diverse and complex phenological patterns (Morellato et al. 2013; Morellato et al. 2000).

Most of the world's plants rely on animal pollination for successful reproduction, especially in the tropics, where the proportion of animal-pollinated species has been estimated at 94% (Ollerton et al. 2011). Floral resources, provided primarily as food rewards for pollination services, can also include substances used for nest construction or aromatic compounds to attract females. The reliable and continuous availability of floral resources in the tropics has enabled strong and diverse adaptations in flower visitors, maintaining rich assemblages of highly specialized floral foragers, such as bees and hummingbirds. Resource extraction by flower visitors is limited to a subset of plants, being constrained by morphology, phenology, and the behaviour of visitors (Rosas-Guerrero et al. 2014). Therefore, spatial and temporal variation in floral resource diversity, abundance and distribution are major structuring factors in pollinator communities (Burkle and Alarcon 2011; Carstensen et al. 2014; Olesen et al. 2008).

Pollinators offer essential pollination services and play a key role in the maintenance of agricultural systems worldwide (Garibaldi et al. 2013), and the interdependency of plant and pollinator populations affects community stability and the productivity of native and agricultural systems (Vázquez et al. 2009). Flowering phenology is therefore highly relevant for the organization and structure of plant communities, the conservation of mutualists and their interactions, and maintenance of essential ecosystem services (CaraDonna et al. 2014; Cruz-Neto et al. 2011; Garibaldi et al. 2013).

3.3. Fruiting and frugivory

Frugivorous animals critically rely on fruits, and fundamental aspects of their ecology — including diet, population size, social behaviour, reproduction, and movements — depend on fruit abundance and seasonality (Hanya and Chapman 2013), which in turn affect seed dispersal and germination effectiveness (Schupp et al. 2010). Neotropical plant species not only bear a high percentage of fruits dispersed by animals, but most tropical vertebrates are frugivores to at least some extent (Hawes and Peres 2014). Therefore, frugivores can be constrained by low fruit production or changes in fruit supply over time (Figure 1c) according to their nutritional content, morphology and colour (Camargo et al. 2013; Develey and Peres 2000; Herrera 2009), with consequences for their conservation and management (Kannan and James 1999). Significant and unexpected crashes in fruit availability can have dramatic effects on vertebrate frugivores. For example, episodic community-wide fruit shortages following an El Niño event greatly elevated mortality of frugivorous and granivorous vertebrates in Barro Colorado Island, Panama (Wright et al. 1999).

Plant conservation is also constrained by growing defaunation scenarios in tropical ecosystems, with cascading consequences for seed dispersal and seedling establishment (Galetti and Dirzo 2013). This is especially critical for large-seeded plant species, given their reliance on large-bodied seed dispersers that are usually the preferred targets of game hunters (Dirzo et al. 2014; Jerozolimski and Peres 2003). For instance, defaunation of large-gaped frugivorous birds has been singled out as the main cause of rapid evolutionary change in palm seed size (Galetti et al. 2013). Though poorly studied, the same evolutionary pressure could affect plant phenology (e.g. favouring a greater overlap between fruiting and the activity of non-hunted frugivores), with far-reaching consequences. Conservation of tropical communities requires an understanding of the interconnection between seasonal fluctuations in climate and the availability of resources for primary consumers (e.g. (Wright and Calderon 2006; Wright et al. 1999), including potential changes induced by both natural (Haugaasen and Peres 2007) and anthropogenic disturbances (Barlow and Peres 2006; Haugaasen and Peres 2007)

3.4. Mismatches in mutualistic networks

The impact of global change on plant phenology is not expected to be uniform across all species, and effects at the species level may lead to consequences at the community level, potentially changing the timing of flowering or fruiting peaks and the duration of reproductive seasons (Donnelly et al. 2011; Hanya and Chapman 2013; Hoye et al. 2013). Furthermore, phenological change in some plant species can potentially affect other plants through competition and/or facilitation for pollinators and seed dispersers, resulting in complex community-wide responses (Burkle and Alarcon 2011). Understanding the higher-order effects of phenological shifts on biotic interactions requires a community level approach, possibly achieved by the application of ecological networks.

Phenology is an important structuring force in plant-animal interactions and influences the topological position of species within mutualistic networks, affecting the organization of interactions and competitive relationships depending on the length and interspecific overlap of reproductive seasons (Encinas-Viso et al. 2012; Olesen et al. 2008, see Figure 1). The length of reproductive seasons is a defining factor in the number of interaction partners a species can have. Some studies indicate that phenology plays a key role in the stability and diversity of mutualistic communities (Thébault and Fontaine 2010) and is of key importance for the management and conservation of plant-pollination interactions and mutualistic networks (Memmott et al. 2007).

In this context, one potential threat from climate change is the temporal uncoupling of mutualistic species interactions (Hegland et al. 2009; Hoye et al. 2013; Memmott et al. 2007). Mismatches between organism and resources, such as plants and their animal symbionts, may arise if climate change affects the onset, peak, and/or duration of flowering and fruiting differentially (Fig. 1C), compared to the activity and life cycles of consumers (Donnelly et al. 2011). Such mismatch can have stark consequences, including recruitment failure in plants and resource scarcity, if not famines and population crashes, in consumers (Berg et al. 2010; Memmott et al. 2007; Wright and Calderon 2006; Wright et al. 1999). Environmental changes that cause some level of mismatch between plants and pollinators can reduce pollination services (Petanidou et al. 2014) and, consequently, seed production (Satake et al. 2013), affecting the dynamics of plant and animal populations (Fig. 1 C). The significance of temporal mismatches in the functioning of ecological communities is inextricably linked to the ability of pollinators and other mutualistic partners to switch their resource use according to the timing of availability. Recent studies indicate great variability in the identity of plant-pollinator interactions (Burkle and Alarcon 2011; Carstensen et al. 2014; Dupont et al. 2009), which could mediate compositional changes driven by phenological mismatches (Kaiser-Bunbury et al. 2010). Changes in the taxonomic composition of visitors due to mismatching between plants and pollinators caused by earlier flowering can affect pollination success and seed set (Rafferty and Ives 2012). Ultimately, both the ability of animal partners to forage on changing host plants as well as the maintenance of viable services for host plants from these mutualistic partners will influence the severity of potential effects of phenological mismatches and the conservation of mutualistic networks (Burkle et al. 2013; Memmott et al. 2007). However, evidence for climate-driven mismatches is at best difficult to obtain and still lacking for most systems (Miller-Rushing and Weltzin 2009).

4. PHENOLOGY, CLIMATE, AND LAND USE CHANGE

4.1. Fragmentation and edge effects

One of the main outcomes of land-use change is habitat loss, which is arguably the main driver of declines in plant and animal diversity (Laurance 2008). Habitat loss and the resulting fragmentation and edge effects produce fine-scale variation in light, temperature and humidity conditions, inducing phenological changes, with consequences to plant-animal interactions and ecological services reverberating throughout the ecosystem (Hagen et al. 2012). Different studies have reported an increase in flowering and fruiting activity in native habitats with increased sunlight, such as edges and gaps (Athayde and Morellato 2014; Burgess et al. 2006; Camargo et al. 2011). However, in fragmented areas and those subjected to edge effects, this higher production in reproductive plant parts does not always favour the reproductive success and recruitment of native species from the original plant community (Athayde and Morellato 2014; Christianini and Oliveira 2013; Quesada et al. 2004). This is probably a consequence of the previously discussed temporal mismatches induced by new environmental conditions, with loss of pollinators and seed dispersers (Hagen et al. 2012). For conservation purposes, phenological studies investigating plant responses to particular environmental conditions, such as natural or anthropogenic edges and forest gaps, would help manage fragmented reserves (de Melo et al. 2006) and model vegetation responsiveness and susceptibility to similar environmental shifts expected in future global change scenarios (Breed et al. 2012; Hagen et al. 2012; Morellato et al. 2013).

4.2. Fire, phenology and conservation

Fire is a natural element of many tropical ecosystems around the world, and often determines vegetation physiognomy and species diversity (Bond and Keeley 2005;

Carvalho and Batalha 2013). Fire disturbance can be either natural or anthropogenic, and the few studies evaluating the effects of fire on phenology have shown that, depending on the plant community, fire can stimulate flowering and fruiting (Pausas et al. 2004) and germination (e.g. Williams et al. 2005), elevate fruit production (Paritsis et al. 2006), and/or accelerate the phenological cycle by shifting the starting date of flowering/fruiting (Paritsis et al. 2006), but may also depress the availability of large-seeded fruits (Barlow and Peres 2006). However, fires can also reduce flowering and fruiting by destroying buds, flowers and fruits, affecting species that reproduce during the fire season (Alvarado et al. 2014; Hoffmann 1998) and/or favour invasive species (D'Antonio 2000). Therefore, fire-induced changes in plant phenology comprise a key issue for vegetation management and conservation.

Phenology can be adopted as a functional trait to characterize plant community responses to fire (Carvalho and Batalha 2013), and predict the dynamics of vegetation recovery or guide management practices and restoration strategies in fire-prone landscapes (Andersen et al. 2005). This has been the case of Ibity New Protected Area (NPA) in Madagascar. Phenology observations showed that high fire frequency reduce flower and fruit production of *tapia* woodlands (Alvarado et al. 2014), indicating the limited potential for natural regeneration of the vegetation (Alvarado et al. 2015). Phenological information has been used to improve the management actions for the Ibity NPA, and is considered as an important issue for the successful implementation of an integrated conservation strategy, targeting restoration of plant communities and reintroduction of threatened plant species.

4.3. Phenological patterns and exotic, invasive and native species interactions

The study of how native, exotic and invasive species (see Richardson et al. 2000 for definitions) interact could benefit from acknowledging plant phenology as a key trait influencing their interactions (Wolkovich and Cleland 2011). Invasive species are managed because they modify the composition and functioning of native ecosystems, driving native species declines or local extinctions (Vilà et al. 2011). Closely related native and exotic species may hybridize if they have matching phenologies, inducing the loss of genetic diversity and disrupting locally adapted populations, such as rare and threatened species (Huxel 1999; Vilà et al. 2000). They may further compete for pollinators and seed dispersers, altering fruit quantity, quality, seed dispersal and thus community structure and ecosystem functioning (Morales and Traveset 2009; Vilà et al. 2000). Exotic species can also leaf out, bloom or produce fruits when natives are not producing alternative resources (thus filling a vacant niche), or can flower or germinate earlier than natives thus benefiting from a priority effect (Wolkovich and Cleland 2011). Both cases (vacant niche and priority effect) affect native species conservation because management can be applied when exotics are vulnerable (e.g. fire, grazing, herbicide, Marushia et al. 2010; Wolkovich and Cleland 2011) and natives are not. Exotics can also leaf or fruit for longer periods of time than natives, sustaining a wider niche, or exhibit greater flowering plasticity, both of which would confer advantages over natives, providing more adaptability to environmental changes with implications for management and conservation (Wolkovich and Cleland 2011).

Native species can act as invasive if disturbances promote biomass growth; e.g. native liana hyperabundance resulting from increased temperature and CO_2 availability associated with global atmospheric change (Phillips et al. 2002; Schnitzer et al. 2014). The phenology of liana-supporting trees may therefore be modified by light competition, affecting leaf, flower and fruit production (Avalos et al. 2007). Conversely, native lianas can play an essential role in providing flower resources to pollinators during periods of scarcity of flowering trees (Morellato and Leitão-Filho 1996). Forest conservation and management in areas with high liana abundance must take into account these potential phenological effects and associated trade-offs.

5. EVOLUTIONARY HISTORY, SPECIES DISTRIBUTIONS AND PHENOLOGICAL VARIABILITY

Deciphering the role of evolutionary history on phenological patterns is important to identify species that are sensitive or resilient to climate change scenarios. Moreover, building more realistic species distribution models based on historical information (from herbaria and/or ground-based phenology) can help to identify changes in plant responses over time and predict their future outcomes. This is especially relevant in systems where available phenological data are restricted to local scales and short time periods as tropical environments in the Southern Hemisphere (Chambers et al. 2013; Morellato et al. 2013).

5.1. Evolutionary history, phenology and conservation

Evolutionary history can affect phenology (Staggemeier et al. 2010; Staggemeier et al. 2015), likely because the physiological pathways triggering reproduction are inherited at an evolutionary timescale (reviewed in Weinig et al. 2014). If evolutionary history matters, closely related species are expected to reproduce under the same environmental conditions; alternatively, if climate is the primary cue, species would reproduce in the most favourable period of time, regardless of their evolutionary relationships (Kochmer and Handel 1986). Current molecular techniques allow us to explicitly examine the evolutionary patterns of species traits and test whether phenology has a strong phylogenetic signal (Staggemeier et al. 2010; Staggemeier et al. 2015). Plants with conservative phenologies are more susceptible to changes in the climatic conditions triggering their reproduction (Willis et al. 2008). Hence, incorporating phenology into predictive models of evolutionary responses to climate change is crucial to identify fragile clades that are more susceptible to global change. Managers and conservationists can then target vulnerable species that do not modify their phenology according to climate, and design effective conservation strategies in light of climatic change scenarios (Miller-Rushing and Weltzin 2009; Willis et al. 2008), especially in complex tropical ecosystems (Staggemeier et al. 2015). Conservation plans can prioritize the protection and maintenance of sensitive species by selecting sites that maximize their persistence.

The timing of reproduction critically defines plant reproductive success, and determines species dynamics, affecting dispersal and colonization rates and the geographic distribution of plants (Chuine and Beaubien 2001). However, the relationships between phenology and species range attributes are underexplored in the literature (Chuine and Beaubien 2001). For example, integrating phenological traits into ecological niche models would result in more representative and reliable projections of the ecology and dynamics of plants and biomes. We advocate combining occupancy records and phenological data archived in historical collections such as herbaria (Lavoie and Lachance 2006) to investigate reproductive phenology at large geographic scales (Zalamea et al. 2011) and in species distribution modelling, to build predictions for future ecosystem alterations and formulate effective conservation strategies (Chapman et al. 2014).

5.2. Variation within populations: why preserve individual variability

Phenological patterns may differ between individuals of the same species, diverging from the average pattern exhibited by the population or community. Intraspecific variation in plant phenology can be related to the micro-environmental conditions where individuals are established, as well as genetic provenance (Herrera 2009; Satake et al. 2013). This is highly relevant in the case of flowering, as it comprises the first mechanism of reproductive isolation; flowering synchrony is critical to the reproductive success of the predominantly out-crossing species in tropical ecosystems (Burgess et al. 2006).

Therefore, assessing the influence of local factors on individual phenology within populations becomes very relevant under current scenarios of global climate change (Diez et al. 2012). Population management and conservation are constrained by the available gene pool and plasticity, which enable species persistence by adaptation and successful reproduction under new environmental conditions. Environmental change reduces the local variability of coexisting conspecifics and hinders their adaptation to new scenarios, as shown for fruit/seed size in arborescent palms (Galetti et al. 2013). Fragmented and spatially isolated habitat patches can remain connected and ecologically functional if their populations maintain ecological interactions and gene flow among individuals across the landscape (D'Eon et al. 2002; Fahrig et al. 2011). Topographical diversity associated with phenological variability in populations of *Centaurea scabiosa* minimise the phenological mismatches with pollinator related to recent climate change (Hindle et al. 2015). Thus, understanding the processes that influence individual phenology and interactions within populations is critical, not only to ensure the viability of these plant populations, but also for the conservation of communities and ecosystems.

6. PHENOLOGY DATABASES, NEW MONITORING TOOLS AND CONSERVATION PRACTICES

6.1. Long-term phenological databases

Phenological monitoring typically falls outside the spectrum of mainstream conservation strategies, although basic phenological data extracted from traditional direct observations of plant populations have provided critical information for conservation planning, at all biodiversity levels defined by the Convention on Biological Diversity (CBD; www.cbd.int/convention/text/)): genes, species and ecosystems. For instance, datasets resulting from phenological studies can be organised as a seed collection calendar, supporting restoration efforts or *ex situ* genetic conservation (e.g. Packard et al. 2005). Also, those data sets make an invaluable contribution for initiatives such as the Kew's Millennium Seed Bank, aiming to harbour the germplasm of up to 25% of the world's plant diversity (Ali and Trivedi 2011). Besides creating a seed collection calendar, the relationship between fruiting phenology and seed germination, dormancy (Garwood 1983; Salazar et al. 2011; Yang et al. 2013), and storage behaviour (Pritchard et al. 2004) in seasonal habitats can be additional criteria for choosing species, methods for breaking dormancy, and seed preservation. Therefore, seeds dispersed at the onset of the rainy season tend to be non-dormant and desiccation-sensitive, while those dispersed during the dry season tend to be dormant and desiccation-tolerant (Salazar et al. 2011; Yang et al. 2013).

From a conservation perspective, phenological research is the basis of several studies, such as the effects of generalized fruiting failure on periodic frugivore famines (e.g. due to El Niño events,Wright et al. 1999), or the importance of the timing of fruiting peaks for breeding seasons of frugivorous birds (Develey and Peres 2000). Also, defining keystone plants for vertebrate fauna during lean times of the year relies on previous knowledge of the phenological patterns of non-redundant resources, compared to alternative resources across the entire plant community (Peres 2000).

Herbaria are a remarkable database and significant source of long-term phenological data that have been used to reconstruct past historical patterns of plant phenology (Hart et al. 2014; Lavoie and Lachance 2006; Primack et al. 2004). Phenological time series from herbarium can be a reliable predictive tool in the context of scarce historical information from ground observation, especially in the tropics (Chambers et al. 2013; Morellato et al. 2013). Therefore, herbarium records can play a key contribution to conservation, providing data on reproductive patterns of single species to whole assemblages across entire regions where no phenological information is available (Bolmgren and Lonnberg 2005; Boulter et al. 2006; Rawal et al. 2015; Tannus and Assis 2004). Considering the growing number of digitalized collections from herbaria all around the world, including some major tropical herbaria, phenological information is available at no cost for managers and conservationists at sites such as the REFLORA, the website for the Brazilian Herbaria collections and species lists (http://reflora.jbrj.gov.br/jabot/PrincipalUC/PrincipalUC.do;jsessionid=52939BFB2B6A0EE6DAE92077C796583F). In addition, one may infer geographic patterns and build phylogeographic models that can offer key insights on the future distribution of endangered and rare species. We can further use herbarium records to identify "phenospecies" (Proença et al. 2012), which can be investigated for shifts in reproductive schedules over time (Borchert 1998; Primack 2014; Rivera and Borchert 2001).

Dendrochronology has been also an effective way to reconstruct longer series of leaf phenology for understudied systems, as the growth rings and cambial activity of tree species are linked to climate (Schweingruber 1996). Although little information is available on tree-ring analysis for tropical trees (Worbes 2002), new methods and tools have increased the reconstruction accuracy of the periodicity of growth ring formation (Roig 2000) and, as a consequence, the prediction of growth seasons and carbon stocks of ecosystems. Dendrochronology and phenology have been applied to understand how climatic variables influence growth and cambial activity of tree species (Brienen et al. 2010), and develop growth models that inform the management and conservation of different tree species (Lisi et al. 2008; Schöngart 2008), including some of the most important non-timber forest products in tropical forests, such as the Brazil-nut tree (Schöngart et al. 2015), which is threatened by systematic overexploitation of mature seeds (Peres et al. 2003). Long-term observations of the cambial phenology may facilitate the interpretation of cell differentiation phases, the length of the growing season and how their growth respond to environmental changes (Rossi et al. 2012). This factor can be critical in cell production and carbon uptake by forests (Rossi et al. 2013).

6.2. Phenological monitoring and new tools

Phenological monitoring techniques continues to grow in tandem with the increasing importance of systematic phenological data to explain ecological patterns, predict the effects of climate change, and address applied environmental and conservation issues (Miller-Rushing and Weltzin 2009). This has led to the development of alternative observation methods (Morisette et al. 2009), such as phenological networks (Betancourt et al. 2005; Fuccillo et al. 2014), remote sensing-based phenology from regional to global scales (Reed et al. 2013), and more recently, deployment of in situ digital cameras for continuous monitoring of multiple simultaneous sites, referred to as near-surface remote phenology (e.g., Richardson et al. 2009; Richardson et al. 2013). Sampling species-rich plant communities can be expensive and labour-intensive in tropical phenology studies, limiting the establishment of comprehensive direct phenological observation systems, and increasing the relevance of alternative techniques such digital repeated photographs (Alberton et al. 2014).

Near-surface remote phenology using digital cameras (“phenocams”) allows the daily detection of leafing events according to changes in the red, green and blue (RGB) channels (Crimmins and Crimmins 2008; Morisette et al. 2009), and have become reliable tools in monitoring leafing changes even in highly diverse vegetation in the seasonal tropics (Alberton et al. 2014).
Orbital remote sensing provides daily to monthly observations of surface radiation, which can be associated to changes in biophysical (e.g. leaf area index) and biochemical (e.g. chlorophyll and water content) vegetation parameters, thereby tracking phenology across space and time (Reed et al. 2013). Remote sensing approaches have proved useful in detecting seasonal vegetation changes over a large range of spatial and temporal scales, and have been incorporated into conservation practices (Nagendra et al. 2013). In the National Park network of Spain, radiometric information derived from the NOAA/AVHRR sensor series was used to assess changes in phenological activity between 1982 and 2006, detecting a decrease in seasonality and the advancing of leaf peak activity (Alcaraz-Segura et al. 2009). In North America, the United States Geological Survey (USGS) is at the forefront on collaborative studies in phenology, combining remote sensing imagery with field-collected datasets obtained by the US Phenology Network (UPN, Graham et al. 2011; Willis 2015). The typical high temporal

frequency of these sensors, although not appropriate for local scale or individuals monitoring, provides valuable phenological information for ecologists and land managers, and support decisions on the allocation of further resources for more detailed spatial assessments (Nagendra et al. 2013; Willis 2015).
Recent developments in remote sensing, such as hyperspectral, hyperspatial, and 3-D remote sensing (LiDAR and InSAR) bring the promise of identifying individual species and directly estimating leaf and canopy traits, which will enable a better coupling with traditional phenology (Reed et al. 2013). More recently, rapid advances in unmanned aerial systems (UAS) have allowed the deployment of these technologies with high temporal repeatability, providing an unparalleled platform for high-resolution phenological data acquisition (Anderson and Gaston 2013). The ability of UAS in providing centimetre spatial resolution data at low cost, and the range of sensors that can be integrated to these systems also have wide applications in conservation science (Colomina and Molina 2014). Paneque-Gálvez et al. (2014) discuss how small drones can support continuous monitoring and aid management and environmental conservation actions, and be easily included in community-based monitoring programs due to its low-cost and ease of operation.

The use of UAS increases monitoring capacity when quantifying land use change, enabling comprehensive ecosystem surveys and monitoring of animal populations at low cost and reduced manpower (Koh and Wich 2012). Furthermore, the use of specific software and algorithms to extract three-dimensional data from low-cost, UAV-based aerial photography, allows the repeated monitoring of several measures related to vegetation structure and complexity, which can help conservationists to address temporal and spatial vegetation dynamics in the landscape and evaluate vegetation recovery for conservation goals (Zahawi et al. 2015).

7. CONCLUSIONS: PROMISING AVENUES FOR FUTURE RESEARCH LINKING PHENOLOGY AND CONSERVATION

Plant reproduction triggers remain poorly understood across the tropics, especially in highly aseasonal ecosystems (Morellato et al. 2013). Recent advances in digital technologies to retrieve historical phenological information from herbaria, satellite images and field cameras will be essential to improve our capability to define proximate triggers, and forecast the effects of climate change. That is the promise of the *e*-phenology Phenology Project (http://www.recod.ic.unicamp.br/ephenology/client/index.html#/), the first tropical initiative to build a network of digital cameras monitoring several vegetation systems in Brazil, while integrating UAVs and remote sensing into phenology monitoring, combined with the traditional on-the-ground direct observations (Alberton et al. 2014; Morellato et al. 2014).

As previously discussed, few studies have confirmed the occurrence of phenological mismatches due to climate or land-use change, and to our knowledge, none of these studies has been conducted in tropical systems, partly because suitable data sets are scarce. Phenology can help identify resource discontinuities along the chronosequence of plant resource availability for consumers that may affect growth and reproduction of target organisms (Schellhorn et al. 2015), and the resulting mismatches in time and space. The understanding and support of ecosystem services provided by biodiversity should take into account the temporal dimension in resource abundance and dynamics across the landscape (Schellhorn et al. 2015).

We therefore propose a series of measures and research topics that can increase the contribution of phenology research to conservation science (Box 1). We have described how phenological studies can support conservation management protocols in actively triggering or accelerating the resilience of degraded ecosystems, potentially making a large contribution to the general research framework on global climate and land-use change. Phenological parameters provide essential measures that can be easily recorded and directly applied to an evolving conservation paradigm centred on preserving ecological processes, rather than a single-minded focus on endangered species or forest structure (Bennett et al. 2009). Recently, phenology was included among the Essential Biodiversity Variables (EBV), defined as “a measurement required for study, reporting, and management of biodiversity change” (GCOS 2010; Pereira et al. 2013). The idea is achieving a global monitoring system that would provide critical data capturing chief elements of biodiversity change, thereby improving conservation management. Phenology as an EBV reaches the criteria of scalability, temporal sensitivity, feasibility, and relevance (Pereira et al. 2013). Remote sensing phenology is highlighted along with the few phenology global networks (Pereira et al. 2013). We also advocate developing other data platforms, especially citizen-science initiatives (Theobald et al. 2015), a denser network of local direct observations, and herbarium data (Lavoie and Lachance 2006; Proença et al. 2012). Those data sources will provide invaluable information to validate remote sensing global patterns and improve biodiversity management and conservation.

The advancements in information science technologies to digitalize herbaria records and retrieve the historical phenological information from herbaria, satellite images and field cameras, will be essential to improve our capability to define proximate triggers and forecast the effects of climate change. The very essence of the importance of recovering historic phenological information, and its wide application for conservation, are illustrated by the work of Primack (2014) on the Thoreau records. As technology evolves and Land Surface Phenology becomes more likely, the ubiquity of ground-based phenology and remote sensing approaches will play an increasingly important role for phenology and conservation. This will help answer questions about the timing and drivers of phenological events under climate and land-cover change scenarios, especially in highly diverse and heterogeneous tropical system.

A final approach concerns the relevance of plant phenology as a tool for conservation education and citizen science as a whole (Fuccillo et al. 2014). Unfortunately, tropical countries have no proposed data acquisition networks or citizen science initiatives that are analogous to important phenological programs in North America (USA – NPN https://www.usanpn.org/ and Cornell Bird Laboratory http://www.birds.cornell.edu/page.aspx?pid=1664); Canada - PlantWatch https://www.naturewatch.ca/plantwatch/) and Europe (United Kingdom - https://www.naturescalendar.org,uk) (Gonsamo et al. 2013) or the new Australian network (ClimateWatch - Australia's National Phenology Network, https://www.climatewatch.org.au). The whole of Latin America, Africa and South-East Asia lacks similar initiatives, but we consider this a worthwhile goal to pursue in the near future. Those networks will become increasingly valuable for conservation managers (Rosemartin et al. 2014) wherever they can obtain cost-effective phenological information, boosting our capacity to preserve natural resources and ecosystem services.

Conflict of interest

The authors declare no conflicts of interest.

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10. TABLE AND FIGURE LEGENDS

Box 1: A brief practical guide for the integration of plant phenology into conservation science

Figure 1. Schematic diagrams exemplifying multiples hypothetical outcomes of human-induced shifts in plant phenology with implications for conservation. Human induced changes on abiotic and biotic factors affect the timing of plant and animal reproductive cycles and mutualistic interactions (A), ultimately with consequences for the conservation of biological diversity. For example, dry seasons that are either longer or more severe than usual (in this hypothetical case from 2 to 4 months) affecting the timing of leafing (B) and reproduction (C), if the trigger for leafing or flowering are the first rains at the end of dry season (e.g. Frankie et al. 1974). In this context, species producing leaves immediately after the first rains would delay leafing activity, thus overlapping with peak insect abundance (B) and, therefore, increasing herbivory damage, potentially affecting plant fitness (Aide 1988, 1993). Flowering delays may result in a reduced overlap between plant flowering and pollinator activity (C). This plant-pollinator mismatch affects plant reproductive success (Hoye et al. 2013; Kudo and Ida 2013; Memmott et al. 2007; Petanidou et al. 2014), and fruit production, with consequences on resource availability for frugivores, which may result in (example of famine in Wright et al. 1999). Low fruit set affects the rates of seed dispersal and plant recruitment, which also occurs later in the wet season (C) (e.g.Kudo and Ida 2013). The hypothetical schemes (A) and (B) can be read at both the species and community levels and considering other potential consequences of climate changes and phenological responses. For example, dry season severity leads to a community level earlier flowering, reducing pollination services.

BOX 1: A BRIEF PRATICAL GUIDE FOR THE INTEGRATION OF PLANT PHENOLOGY INTO CONSERVATION SCIENCE

Conservation practice	Phenological data sources	Ecological scale	Examples
Establishment of a calendar for collection of seeds and other plant resources for *in situ* or *ex situ* conservation	Direct ground observation of plant phenophases (e.g. leafing, flowering, fruiting) and their interaction with local environmental variables;	Population/species	Kew's Millennium Seed Bank Project uses information on fruiting, seed germination, dormancy and storage for appropriate *ex situ* conservation techniques of over 27,000 plant species (Ali and Trivedi 2011)
Knowledge on the flower/fruit production of a threatened plant species to support conservation strategies	Qualitative and/or quantitative estimate of flower and/or fruit production over time	Population/species	Study focused on the phenology of the rare species (e.g. *Horsfieldia kingii*) showed limited availability of fruits for its main seed disperser (Datta and Rane 2013)
Increase of intra-population diversity and gene pool		Population/species	Topographical variation reduced chances of phenological mismatches between *Centaurea scabiosa* and its pollinator (Hindle et al. 2015).
Maintain the resource availability in time and space to preserve pollination vectors and support ecosystem services	Flowering and fruiting phenology at different scales	Community/ population/species	Managing natural and agricultural landscapes for continuous resource availability for pollinators, thereby maintaining ecosystem services (Schellhorn et al. 2015)
Control herbivory population and damage,	Leafing of host plant species and phenology of phytophagous insects	Population/species	Years of high synchrony of leaf-feeding Lepidoptera and leafing peaks cause herbivore outbreaks. Disruption of the synchrony between herbivores and their host plants caused by climate change may affect population viability if synchronicity is not restored (van Asch and Visser 2007).
Harvesting sustainability of non-timber forest products	Information on flowering and fruiting time and fruit/seed crop size	Population	Seed and flower phenology surveys over a large geographic area, ethno-ecological interviews, and harvest experiments to guide sustainable management of the Brazilian golden-grass (Syngonanthus nitens – Eriocaulaceae, Schmidt et al. 2007)
Maintenance of animal populations critically depending on fruit resources for survival	Seed traps: timing and fruit/seed crop size	Community	Vertebrate frugivore famines in Barro Colorado Island, Panama, as consequence of abnormally low fruit production associated with an El Niño event (Wright et al. 1999)
Detection of potential keystone plant species		Community	Data from 8 years of seed-fall enabled distinguishing seven keystone species that bear disproportionally important resources during periods of scarcity at Cocha Cashu, Manu National Park, Peru (Diaz-Martin et al. 2014)
Conservation plans considering not only target species but also their ecological interactions	Phenology of plant species and their mutualistic and antagonistic interactions (e.g. pollinators, seed dispersers, parasites)	Community	Plant-pollinator interactions are strongly determined by phenology (Olesen et al. 2008)
Assessing impacts of climate change on plant species phenology to guide mitigation actions	Long-term phenological time series from herbarium collections and historical records	Species	Reconstruction of a long-term phenological pattern of a high-value medicinal herb of the Indian Himalayan Region to understand climate change effects (Gaira et al. 2011).
	Flowering and fruiting time from herbarium collections	Community, landscape and ecosystem	Accessing fruiting and flowering phenology and climatic triggers at large scales (Bolmgren and Lonnberg 2005; Boulter et al. 2006).

Conservation practice	Phenological data sources	Ecological scale	Examples
Estimates of carbon stocks and development of growth models that provide baseline ground information for the management and conservation of different tree species	Phenology of plant growth from dendrochronological approaches	Species, landscape and ecosystem	Long-term observations of the cambial phenology showed growth responses to environmental changes (Rossi et al. 2012).
Forecasting groups of plants more vulnerable or resilient to climate change to set effective priorities for conservation agendas.	Phenological data within a phylogenetic/evolutionary context	Community	Analysing the phenology of the Neotropical Myrtaceae using a phylogenetical framework detected the species sharing a more conservative phenology, thus elucidating the principal candidates for conservation initiatives (Staggemeier et al. 2015)
Identification of early colonists that can facilitate the establishment of latecomers by amplifying the trophic resource base for frugivores operating as effective seed vectors	Plant phenology across successional chronosequences	Community	Long-lived pioneers that bear keystone resources (e.g. ripe fruits) over extended fruiting seasons, such as several neotropical arborescent palms; species exhibiting intra-population fruiting asynchrony are instrumental in sustaining a large coterie and aggregate biomass of generalist frugivores throughout the year (Peres 1994a, b)
Evaluation of community-wide responses to disturbances (including wildfires, invasions of exotic species, proliferation of edge effects) and their recovery	Plant phenology monitoring of ecosystem disturbances	Community, landscape and ecosystem	High fire frequency reduced flower and fruit production of *tapia* woodlands in Madagascar, decreasing the potential for natural regeneration (Alvarado et al. 2014)
Large amount of phenological information on a cost-effective way that can be used by conservation managers	Phenological information from citizen science	Ecosystem and planetary	PlantWatch programme of Canada allows monitoring and tracking of climate change (Gonsamo et al. 2013)
Monitoring vegetation changes to detect vegetation recovery and resilience to natural and anthropogenic disturbances	Near-surface remote phenology using digital cameras ("phenocams")	Landscape and ecosystem	Monitoring: fire incidence and resilience in fire-prone ecosystems; vegetation recovery and restoration
Spatially explicit measurement of vegetation responses to climatic factors and disturbances over multiple spatial and temporal scales	Remote sensing of plant phenology	Ecosystem and planetary	The US Geological Survey (USGS) combines remote sensing imagery with phenological field-collected datasets obtained by the US Phenology Network (UPN, Graham et al. 2011; Willis 2015)

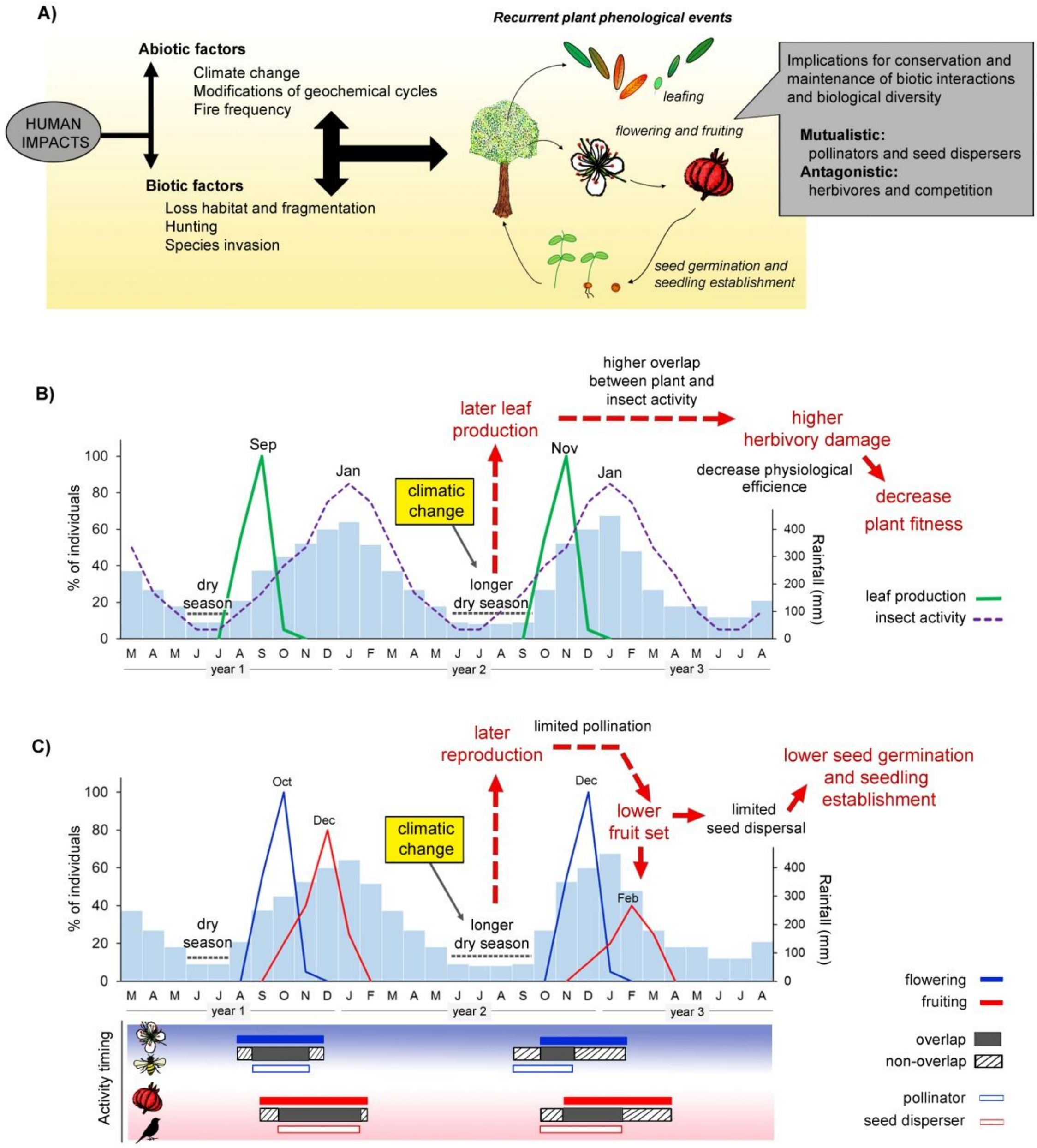

Figure 1. Schematic diagrams exemplifying multiples hypothetical outcomes of human-induced shifts in plant phenology with implications for conservation. Human induced changes on abiotic and biotic factors affect the timing of plant and animal reproductive cycles and mutualistic interactions (A), ultimately with consequences for the conservation of biological diversity. For example, dry seasons that are either longer or more severe than usual (in this hypothetical case from 2 to 4 months) affecting the timing of leafing (B) and reproduction (C), if the trigger for leafing or flowering are the first rains at the end of dry season (e.g. Frankie et al. 1974). In this context, species producing leaves immediately after the first rains would delay leafing activity, thus overlapping with peak insect abundance (B) and, therefore, increasing herbivory damage, potentially affecting plant fitness (Aide 1988, 1993). Flowering delays may result in a reduced overlap between plant flowering and pollinator activity (C). This plant-pollinator mismatch affects plant reproductive success (Hoye et al. 2013; Kudo

and Ida 2013; Memmott et al. 2007; Petanidou et al. 2014), and fruit production, with consequences on resource availability for frugivores, which may result in (example of famine in Wright et al. 1999). Low fruit set affects the rates of seed dispersal and plant recruitment, which also occurs later in the wet season (C) (e.g.Kudo and Ida 2013). The hypothetical schemes (A) and (B) can be read at both the species and community levels and considering other potential consequences of climate changes and phenological responses. For example, dry season severity leads to a community level earlier flowering, reducing pollination services.

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Reviewers' comments:

Reviewer #3: BIOLOGICAL CONSERVATION- BIOC-D-15-00602R1

This is a timing review on phenology studies, an issue that has become topical in recent years because its relevance to understand population responses to global change. Certainly, an increasing number of ecological studies show the importance of a fine characterization of the phenophases of a plant community to understand their functioning and predict their functional responses to different triggers of global change.

The MS is well written, integrates interesting different aspects of plant phenology and provide a guide to include phenology in prospective long-term studies and management plans. Therefore the study is of general interest for a wide audience, particularly for Biological Conservation readers.

Next, I suggest some changes to improve the current version of the MS

1. Authors comment the effect of climate and land use change on Section 4. For example, they argue that edge effect "increase of flowering and fruiting activity" (Line #389) or fragmentation affect reproductive success. Yet, these are functional responses of plant populations to different types of disturbances/changes, but they do not necessary entail changes in phenology. Please, review the MS and make sure that you only include examples that make the case for phenological shifts in response to climate and land use changes.

Response: *Thanks for the comment. We completely understand the reviewer's concern, but we have long used a broader conceptual definition of phenological changes which should not only represent shifts in the timing of reproduction but also shifts on the intensity (amplitude) and duration of plant phenophases. Therefore, increases in flowering and fruiting activity can indeed be considered phenological responses to a given environmental cue. In the paper we refer to elevated levels in reproductive effort (i.e. more frequent, longer, or more intensive flowering and fruiting activity) in plants within edge-dominated habitats. These in our view are 'real' resource allocation shifts within the metabolic pathway alternatives available to plants, so we see them as true phenological responses. We agree that the effect on plant reproductive success is a functional response that is a consequence of a phenological shift, as reported in the text. We further reviewed and double-checked the text to make sure we only include examples of phenological shifts in response to climate change and land use change as suggested.*

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2. Section 3.2 Flowering and pollinators could some recent findings that correlated fragmentation with pollinator movement patterns and fecundity levels in forest species (Breed et al. 2012; Breed, Christmas & Lowe 2014)

Response: *We thank you for the suggestion and we have added one of the suggested references (Breed et al. 2012).*

3. There are some weird expressions: "the fabric of interactions and competitive relationships" (Line#345)

Response: *We do not see this as "weird", but may be too poetic. We have therefore rephrased the text to: "the organization of interactions and competitive relationships"*

4. Besides environmental changes such as temperature, phenology also responds to invariant clues, such as photoperiod. Please, comment the effect of these opposes forces.

Response: *We include a sentence regarding the importance of photoperiod as an invariant clue to define the timing and periodicity of plant phenology of tropical environments with low* climatic seasonality (Lines#135 to 141).

5. There are interesting concepts along the MS that should be presented in the introduction. The introduction section should include a brief overview about phenospecies or the idea of including phenology as a functional trait, or about niche changes.

Response: *Thank you for the suggestion. We have therefore incorporated into the introduction the additional concepts pointed out by the reviewer and removed any repetition from the main text.*

Reference included:

Breed, M.F., Gardner, M.G., Ottewell, K.M., Navarro, C.M. & Lowe, A.J. (2012) Shifts in reproductive assurance strategies and inbreeding costs associated with habitat fragmentation in Central American mahogany. Ecology Letters, 15, 444-452.

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Figure
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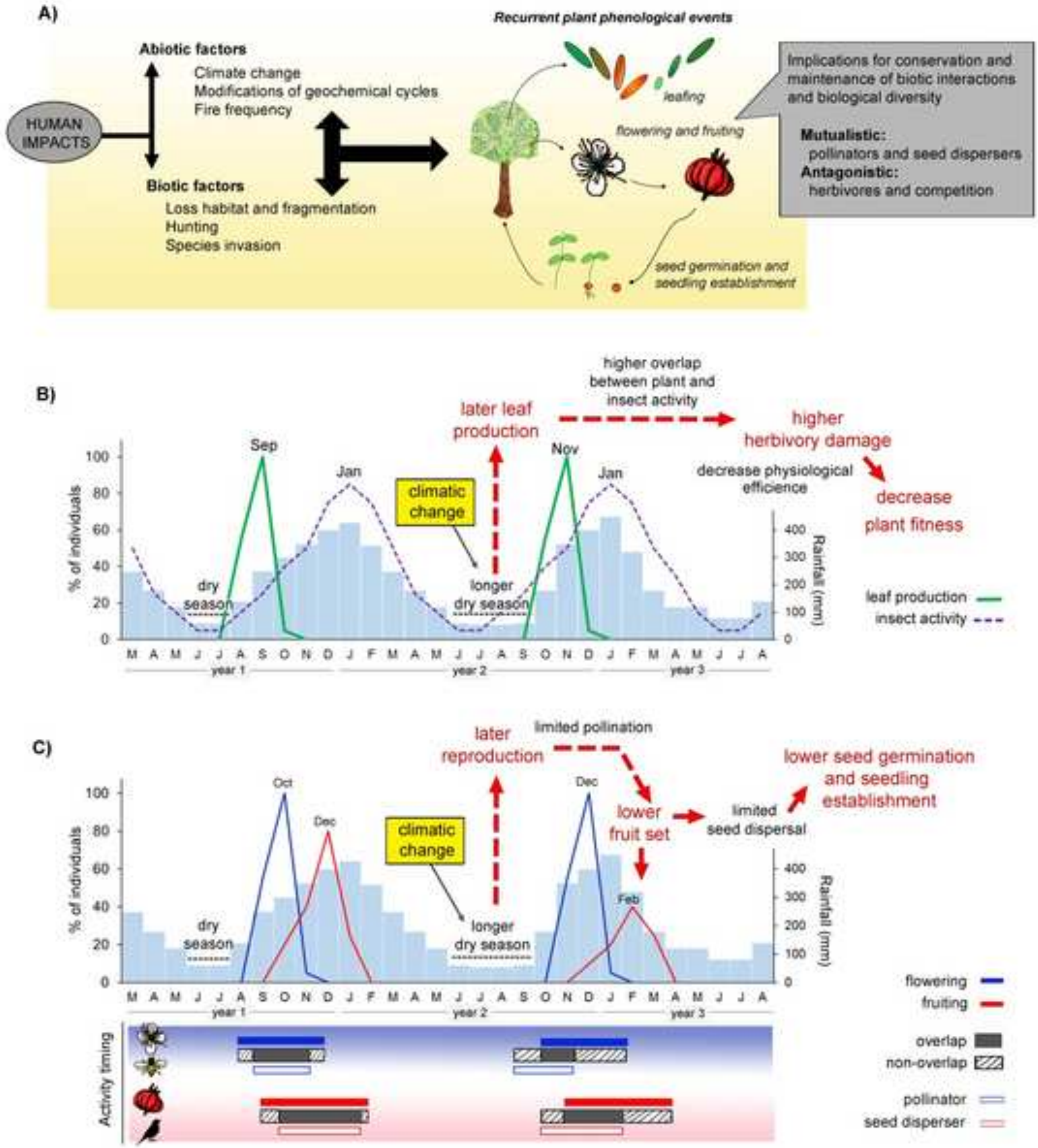

Graphical Abstract