Impacts of climate change and management responses in tropical forests depend on complex frugivore-mediated seed dispersal

Karel Mokany1*, Soumya Prasad2 and David A. Westcott3

ABSTRACT

Aim Biodiversity outcomes under global change will be influenced by a range of ecological processes, and these processes are increasingly being considered in models of biodiversity change. However, the level of model complexity required to adequately account for important ecological processes often remains unclear. Here we assess how considering realistically complex frugivore-mediated seed dispersal influences the projected climate change outcomes for plant diversity in the Australian Wet Tropics (all 4313 species).

Location The Australian Wet Tropics, Queensland, Australia.

Methods We applied a metacommunity model (M-SET) to project biodiversity outcomes using seed dispersal models that varied in complexity, combined with alternative climate change scenarios and habitat restoration scenarios.

Results We found that the complexity of the dispersal model had a larger effect on projected biodiversity outcomes than did dramatically different climate change scenarios. Applying a simple dispersal model that ignored spatial, temporal and taxonomic variation due to frugivore-mediated seed dispersal underestimated the reduction in the area of occurrence of plant species under climate change and overestimated the loss of diversity in fragmented tropical forest remnants. The complexity of the dispersal model also changed the habitat restoration approach identified as the best for promoting persistence of biodiversity under climate change.

Main conclusions The consideration of complex processes such as frugivore-mediated seed dispersal can make an important difference in how we understand and respond to the influence of climate change on biodiversity.

Keywords Australia, beta-diversity, composition, diversity, fruit, metacommunity, model, plant, restoration, richness.

INTRODUCTION

A substantial research effort has focused on projecting outcomes for biodiversity under scenarios of global change (Araújo et al., 2011; Bellard et al., 2012; Warren et al., 2013). This research is critical for clarifying the level of threat facing biodiversity, and in helping to identify conservation and management actions that are likely to best promote the persistence of biodiversity into the future. Given the key role that this research plays, it is increasingly recognized that biodiversity projections need to become more robust and better incorporate those ecological processes likely to strongly influence future outcomes, such as dispersal and interspecific interactions (Thuiller et al., 2008; McMahon et al., 2011; Wisz et al., 2013).

Although there is widespread recognition of the importance of incorporating ecological processes in projecting outcomes for biodiversity under global change, relatively few modelling approaches have emerged that address this need. Some of the
most promising approaches combine correlative and mechanistic components in 'hybrid' modelling techniques, which account for processes such as dispersal and metapopulation dynamics (Cheung et al., 2008; Keith et al., 2008; Anderson et al., 2009). Given the reasonably intense requirements of these hybrid approaches in terms of information, modelling effort and expertise, their application has been restricted to projecting outcomes for a relatively small number of well-studied species (McMahon et al., 2011; Bateman et al., 2013). These hybrid approaches are less suitable where there is a broader conservation focus and the interest is in understanding potential outcomes for communities or 'biodiversity as a whole' (Margules & Pressey, 2000; Mokany & Ferrier, 2011). This is especially the case in highly diverse and poorly studied systems, such as tropical forests (Carson & Schnitzer, 2008; Feeley & Silman, 2010).

Where we require biodiversity projections relevant to large numbers of poorly studied species, community-level modelling approaches may be more suitable (Ferrier & Guisan, 2006; Mokany & Ferrier, 2011). One recently developed approach projects change in the composition of all communities across a region (i.e. each cell in a regular spatial grid) dynamically over time (Mokany et al., 2012). This approach applies a general metacommunity model (M-SET) that explicitly incorporates dispersal, community assembly and inherent community-level constraints in simultaneously projecting outcomes for all species in a taxonomic group across large regions, under alternative scenarios (e.g. climate change, habitat configuration) (Mokany et al., 2012, 2013).

To date, the application of this metacommunity modelling approach has assumed that all species within a taxonomic group have the same dispersal capacity, which remains constant over space and time. While this is a convenient assumption for modelling purposes, it is unlikely to reflect the reality of complex systems such as tropical plant communities, where a large proportion of species have their seeds dispersed by frugivorous vertebrates (Cortes & Uriarte, 2013). In these systems, the dispersal of plants with different fruit types depends on the abundance of different frugivores, their fruit consumption patterns, gut passage time and movement behaviour (Dennis & Westcott, 2007; Guttal et al., 2011). Consequently, the dispersal capacity of plants with different fruit types varies over space (Cortes & Uriarte, 2013), and is predicted to change dramatically into the future as climate change influences the abundances of key frugivores (McConkey et al., 2012; Mokany et al., 2014a). Given that no studies have incorporated such realistically complex dispersal processes in projecting outcomes for a diverse and relatively poorly studied group such as tropical plants, it remains unclear whether biodiversity models need to account for these dispersal processes, or whether simple approximations are sufficient.

Here we incorporate complex frugivore-mediated dispersal processes into the M-SET metacommunity model to project climate change outcomes for plant diversity in the Australian Wet Tropics (all 4313 plant species). Our approach utilizes one of the world’s best data sets on frugivory and seed dispersal (Westcott et al., 2005; Dennis & Westcott, 2006, 2007) to provide the most realistic consideration currently possible for how frugivores are likely to influence changes in plant diversity in this region. We use this approach to assess how projected outcomes for plant biodiversity under climate change differ when dispersal models of varying complexity are applied. Finally, we examine how the complexity of the dispersal model influences which approach to tropical forest restoration is predicted to best promote the persistence of plant biodiversity into the future.

**METHODS**

**Study area**

The Australian Wet Tropics region modelled in our study included the Wet Tropics Bioregion in Queensland, Australia (from IBRA, 2012) and a 100-km buffer around it (approximately 14°39’ S to 20°24’ S and 143°53’ E to 147°30’ E) (Fig. S1 in Supporting Information). Of the 87,365 km² land area within this region, 95.2% is natural vegetation (as classified by Queensland Land Use Mapping, 1999), with the area protected for conservation comprising 17.6% of the study region and 44.2% of the Wet Tropics Bioregion (as defined by CAPAD, 2010). Our analyses were conducted on a 250-m resolution spatial grid over this region, as defined by the Australian GEODATA 9 Second Digital Elevation Model V3.

**Metacommunity modelling**

We applied a dynamic macroecological modelling approach (Mokany et al., 2012) to project outcomes under climate change for the native flora of the Australian Wet Tropics (all 4313 plant species) (Fig. S2). This approach first involved deriving correlative models of species richness ($P < 0.001$, proportion deviance explained ($D^2 = 0.407$) and pairwise compositional dissimilarity ($P < 0.001$, $D^2 = 0.342$) using 527 plant community survey plots (500–1000 m²) and complete spatial environmental data at 250-m resolution across the Australian Wet Tropics ($87,365$ km²) (Mokany et al., 2014b). These models of species richness and compositional dissimilarity were combined with the survey data plus 104,831 plant species occurrence records to predict the current composition of all communities (grid cells) across the Australian Wet Tropics (> 1.3 million grid cells), using the DynamicFOAM algorithm (Mokany et al., 2011, 2014b). The 10 replicate DynamicFOAM predictions of current metacommunity composition possessed patterns in compositional turnover that closely matched those expected from the underlying model of pairwise compositional dissimilarity (mean absolute error in Sørensen’s dissimilarity of $0.05 \pm 1.9 \times 10^{-4}$) (Mokany et al., 2014b).

These predictions of current plant community composition across the Australian Wet Tropics were used as the starting point for the M-SET metacommunity model (Mokany et al., 2012, 2013). M-SET is a dynamic, spatially explicit model that predicts change in the composition of every community (presence/absence of each species in a grid cell) across a region over time,
Dispersal and climate change outcomes

We applied three alternative dispersal scenarios in the M-SET metacommunity model (Fig. S3). The most complex dispersal scenario (‘space and time’) accounts for the role of 45 important frugivorous vertebrates (birds, bats, arboreal marsupials) in influencing dispersal kernels for fleshy fruited plant species (Mokany et al., 2014a). The projected abundances of the 45 frugivore species at each point in time and space influences the proportion of fruit eaten by each species (which varies across seven plant fruit types) and hence the distances that seeds are dispersed, accounting for differences in the gut passage time and movement behaviour of each frugivore species (Westcott et al., 2005; Dennis & Westcott, 2006, 2007; Mokany et al., 2014a). Differences in movement behaviour of each frugivore species between contiguous and fragmented habitat are also accounted for (Mokany et al., 2014a). To implement the space and time dispersal scenario we applied the approach presented by Mokany et al. (2014a), with the abundances of the 45 frugivore species projected for each decade between 2010 and 2100, with abundances for non-decadal years (i.e. 2xx1 to 2xx9) linearly interpolated between the two closest decadal projections. For wind-dispersed plant species in this scenario, we applied a two-dimensional negative square power-law model of dispersal probability from site i to site j (Pd_{ij}) as a function of distance between them (r_{ij}), which has previously been implemented as the dispersal model in M-SET (Mokany et al., 2012, 2013):

$$Pd_{ij} = \frac{1}{2\pi r_{ij} \pi \lambda} \frac{2K}{1 + (r_{ij}/\lambda)^2}$$

The parameters for this kernel applied to wind dispersal were maintained constant over space and time, with median dispersal distance $\lambda = 5$ m and scaling parameter $K = 13$ (Mokany et al., 2014a) approximated from Bullock (2012).

The second dispersal scenario (‘space’) applies the same complex dispersal kernels as in the space and time scenario but does not account for the effects of climate change in influencing the abundance of frugivores over time, and hence ignores possible temporal change in dispersal kernels for each location (Fig. S3). Therefore, the space dispersal scenario applies the frugivore-mediated dispersal kernels projected for the present (2010) across the whole simulation, ignoring the effects of climate change on these kernels (Mokany et al., 2014a).

The third dispersal scenario (‘passive’) ignores the specific role of different frugivores in dispersing seeds and applies a single dispersal kernel to all plant species in all locations over time: the negative square power-law model of dispersal probability (equation 1) as a function of distance (Mokany et al., 2014a) (Fig. S3). We derived parameters for this dispersal kernel that approximated the average level of dispersal in the ‘space’ dispersal scenario by applying the spatially explicit dispersal kernels in the space scenario to determine the average median dispersal distance and average summed dispersal probability across all 4313 plant species and all grid cells, considering the 10-km radius around each grid cell. For the kernel in the ‘passive’ dispersal scenario, the median dispersal distance ($\lambda$) applied was 13.5 m and the scaling parameter ($K$) applied was 24, with a maximum dispersal distance of 10 km considered in each year of the simulation (as with all other dispersal scenarios).

For each combination of climate change and dispersal scenario, we applied 20 replicate M-SET simulations: two replicates for each of the 10 predictions of current plant community composition. The results presented are summaries over the replicate simulations within a climate change/dispersal scenario ‘treatment’. Only habitat (grid cells) currently considered as natural vegetation was included in the primary simulations, and we assumed that this remained constant throughout the simulation. To account for the regional edge effects in our simulations, we applied the model to the full region but omitted any grid cells within 50 km of the region boundary prior to analysing and mapping our results.
**Restoration scenarios**

To assess how the dispersal scenario may influence decisions regarding the management of biodiversity under climate change we applied additional simulations using M-SET to consider restoration of ‘modified habitat’ (human land use) in the Atherton Tablelands region of the Australian Wet Tropics (Fig. S4). We chose this area because we have previously identified it as an area of high conservation value (Mokany et al., 2014b) and because of the high levels of clearing that have occurred here (Fig. S4). Within the 2156-km² focal region, we allocated 2% (10.2 km²) of the currently modified habitat to restoration, using four alternative configuration approaches (Fig. S4): (1) purely random allocation (‘random’); (2) random allocation along the edge of contiguous habitat (‘contiguous’); (3) random allocation along the edge of fragmented habitat (‘fragments’); and (4) allocated as 250-m (one grid cell) wide corridors connecting fragmented habitat with contiguous habitat by the shortest distance, with priority given to connecting larger fragments over smaller fragments (as in Mokany et al., 2013) (‘corridors’).

For the grid cells allocated as restored habitat, we linearly increased their potential species richness in the simulation from 10% of that predicted by the species richness model at the beginning of the simulation to 100% of that predicted by the species richness model after 50 years of the simulation. This rate of increase in the number of plant species supported in restored tropical forests approximates trends observed by Martin et al. (2013). We applied the M-SET model to the Atherton Tablelands region and a 50-km buffer around it for all combinations of restoration approach \((n = 4)\) and dispersal scenario \((n = 3)\). Given the number of simulations required, we considered a single climate scenario (CSIRO mk3.5, A1FI) and applied a single simulation for each of the 10 predictions of initial plant community composition (i.e. 10 replicates per combination of restoration and dispersal scenario).

**RESULTS**

**Influence of dispersal on biodiversity outcomes**

Incorporating the effects of the influence of frugivores on seed dispersal had a more substantial influence on projected plant biodiversity outcomes in the Australian Wet Tropics than did applying a very different climate change scenario (within the A1FI emissions scenario). For example, the median area of occurrence across all 4313 plant species reduced by 54.4% to 2100 under the space and time dispersal model and hot/dry climate scenario (Fig. 1). Applying the hot/wet climate change scenario to the same dispersal model improved this to a 17.3% median loss of area of occurrence (Fig. 1). In contrast, applying the passive dispersal model to the hot/dry climate scenario resulted in a 5.5% increase in the median area of occurrence of Australian Wet Tropics plant species, and a 32.7% increase under the hot/wet scenario (Fig. 1). There were relatively minor differences in projected outcomes for plant biodiversity between the two dispersal scenarios that considered the role of frugivores in dispersing seeds. The difference between the ‘space’ and the ‘space and time’ dispersal scenarios, in terms of the median change in area of occurrence, was less than 1% for both the hot/dry climate scenario (−55.2% and −54.4%, respectively) and the hot/wet climate scenario (−17.5% and −17.3%, respectively) (Fig. 1).

Accounting for frugivore-mediated dispersal increased the variation between plant species in terms of their projected change in area of occurrence under climate change. As expected, applying the same ‘passive’ dispersal kernel to all species resulted in all plant fruit groups having a very similar change in their area of occurrence over the simulation (Fig. 2a, d). When differences in dispersal kernels between plant fruit groups were considered over space (Fig. 2b, e) as well as time (Fig. 2c, f), plant species in the fruit groups ‘small fig’, ‘fig’, ‘multiple fruit’ and ‘small drupe’ were projected to more than double their current area of occurrence under climate change, on average. In contrast, those plant fruit groups that are primarily wind dispersed (‘small dry’, ‘dry’, ‘sori’), comprising two-thirds of all plant species in the region, suffered projected reductions in their area of occurrence under climate change (Figs 2 & S5).
At the community level, the overall projected change in species richness of communities (net flux of species) under climate change (space and time dispersal scenario) was an average loss of 10.2 species per community for the hot/dry scenario (range −199 to +197) (Fig. 3a) and an average gain of 41.6 species per community for the hot/wet scenario (range −171 to +278) (Fig. S6). The greatest projected loss of plant species was in the southern Atherton Tablelands (elevation 500–1100 m; Fig. S1) under both the hot/dry (Fig. 3a) and the hot/wet climate change scenarios (Fig. S6a), with species richness falling by as much as 40%. In contrast, low-elevation forests (elevation <600 m) in the Daintree region in the north of the Australian Wet Tropics (Fig. S1) were projected to gain up to 200 species per 250-m grid cell (an increase of up to 80%) under the hot/dry climate scenario (Fig. 3a) and up to 278 species under the hot/wet scenario (an increase of up to 95%) (Fig. S6a).

Applying the ‘space’ dispersal scenario resulted in similar spatial projections of net flux of species over time, with a slight over-prediction of community species richness in 2100, compared with the ‘space and time’ scenario (Fig. 3b) (mean +0.01, range −5 to +59). Applying the much simpler ‘passive’ dispersal scenario resulted in areas with substantially different spatial projections of net flux of species over time compared with the space and time dispersal scenario (mean −0.37, range −200 to +68), with dramatic under-prediction of future species richness of rain forest fragments in human-modified landscapes (Fig. 3c). These general differences between dispersal scenarios were also observed under the hot/wet climate change scenario (Fig. S6b, c). For individual plant fruit groups, differences in their median response to climate change under alternative dispersal scenarios (Fig. 2) were matched by spatial projections of the change in number of species represented by each group in each community (grid cell) (e.g. Figs S7 & S8).

For the space and time dispersal scenario, predicted community compositional turnover (Sørensen’s dissimilarity) under climate change was much greater in the hot/dry climate scenario (mean 0.46, range 0.25–0.81) (Fig. 4a) than in the hot/wet climate scenario (mean 0.32, range 0.10–0.77) (Fig. S9). For both climate scenarios, compositional turnover was greatest in higher-elevation areas (>600 m) and lowest in low-elevation areas (<600 m) (Fig. S10). Under the ‘space’ dispersal scenario, community compositional turnover was projected to be slightly greater (mean +0.004, range −0.12 to +0.06) (Fig. 4b), while
under the ‘passive’ dispersal scenario, compositional turnover was projected to be markedly lower (mean \(-0.071\), range \(-0.25\) to \(+0.29\)) (Fig. 4c). These general differences between dispersal scenarios were also observed under the hot/wet climate change scenario (Fig. S9b, c).

**Influence of dispersal on outcomes under restoration**

Our assessment of four alternative configurations of tropical forest habitat restoration in the Atherton Tablelands area of the Australian Wet Tropics found that the potential benefits of restoration, and the ranking of restoration configurations, varied under the different dispersal scenarios (Table 1). Under the ‘passive’ dispersal scenario, restoring habitat in corridors that connect existing habitat achieved the greatest gain in the area of occurrence per species (0.89 km\(^2\)), whereas restoring areas adjacent to existing contiguous habitat performed the best under both the ‘space’ dispersal scenario (0.84 km\(^2\) per species) and the ‘space and time’ dispersal scenario (0.81 km\(^2\) per species) (Table 1). In contrast, random (ad hoc) restoration of tropical
forest habitat consistently performed poorly across all dispersal scenarios (Table 1).

**DISCUSSION**

Incorporating important ecological processes into biodiversity models is a priority for research if we are to improve the robustness of future projections (Thuiller et al., 2008; McMahon et al., 2011; Wisz et al., 2013). However, the level of model complexity required to sufficiently capture the relevant dynamics remains unclear (Van Nes & Scheffer, 2005), particularly for complex processes such as frugivore-mediated seed dispersal in diverse tropical forests (Westcott et al., 2005; Côrtes & Uriarte, 2013). Here we have demonstrated that accounting for frugivore-mediated dispersal processes in the Australian Wet Tropics substantially changed projected plant biodiversity outcomes and altered the restoration management approach predicted to be most effective in promoting biodiversity under climate change.

Our results show that considering realistic frugivore-mediated seed dispersal had a greater effect on the projected change in area of occurrence for all 4313 plant species than did a dramatically different climate change scenario (Figs 1 & 2). Simplifying the complexities of frugivore-mediated seed dispersal into a single summary dispersal kernel for all plant species over space and time (‘passive’) overestimated the change in area of occurrence for most species, suggesting minor benefits under the hot/dry climate scenario (median gain 5.5%) as opposed to substantial projected losses when complex dispersal processes were considered (median loss 54.4%) (Fig. 1). Indeed, accounting for interspecific differences in dispersal processes resulted in much greater variation between species in their projected outcomes compared with when all species possessed the same dispersal capacity (Figs 1 & 2). These results suggest that large differences in the dispersal capacity of species are likely to precipitate large differences in the outcomes for those species under climate change (e.g. Figs S5, S7 & S8), and in such cases a neutral assumption that all species have identical dispersal capacities (Hubbell, 2001; Mokany et al., 2012) is overly simplistic.

Projected community-level outcomes for plant biodiversity in the Australian Wet Tropics show the greatest compositional turnover and loss of species richness along the drier western edge of the current tropical forest (Figs 3 & 4), consistent with a contraction of rain forest and expansion of savanna (Marengo et al., 2011). These projections were consistent across climate scenarios (Figs S6 & S9), as were the projected gains in species richness and relatively low compositional turnover in tropical forests of the Daintree region, in the north of the Australian Wet Tropics (Figs 3 & 4). The substantial increases in potential species richness projected in lowland areas such as the Daintree region should be interpreted with caution, given the novel climate space these areas are predicted to experience in the future. However, our results broadly align with previous research in the Australian Wet Tropics (Hilbert et al., 2001), suggesting the greatest negative effects of climate change on tropical forest diversity at mid to high elevations (> 600 m; Figs S10 & S11) with impacts on lowland rainforest being marginal or positive.

When the simpler ‘passive’ dispersal model was applied there were systematic deviations in the projected biodiversity outcomes at the community level. The first major difference was a much reduced predicted species richness of fragmented tropical forests within human-modified landscapes under the simple ‘passive’ dispersal scenario (Fig. 3c). This result suggests that frugivores are likely to play an important role in facilitating seed dispersal to and from fragmented patches of tropical forest, enabling species to shift their distributions into and out of these habitats as the climate changes (McConkey et al., 2012). The simplistic ‘passive’ dispersal model also systematically underestimated plant community compositional turnover in contiguous habitat of the Australian Wet Tropics (Fig. 4c). Accounting for realistic frugivore-mediated seed dispersal (‘space and time’) may result in higher levels of projected community compositional turnover than the simpler dispersal assumption ( ‘passive’) due to more rapid shifts in the distributions of some species under climate change, facilitated by frugivores increasing the likelihood of long-distance dispersal events (Nathan et al., 2008; Mokany et al., 2014a).

Direct consideration of the role of frugivores in dispersing seeds strongly influences the projected outcomes for plant biodiversity. However, our results suggest that incorporating the substantial effects of climate change on frugivore abundances (‘space and time’) (Mokany et al., 2014a) produces relatively minor differences compared with holding the current (2010) spatially explicit frugivore-mediated dispersal kernels constant into the future (‘space’). Specifically, the projected changes in the area of occurrence of plant species (Figs 1 & 2b, c, e, f) and the spatial projection of changes in species richness (Fig. 3b) and community compositional turnover (Fig. 4b) were broadly consistent regardless of whether change in frugivore abundances over time were considered. Despite the large projected reductions in median and long-distance dispersal under climate change (Mokany et al., 2014a), our results suggest there may still

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be sufficient levels of dispersal in most areas to enable plant species to shift their distributions and for communities to reassemble. Applying current (2010) frugivore-mediated dispersal kernels across the whole simulation (2010–2100) does result in overestimation of the dispersal capacity of some plant fruit groups when compared with applying the climate change-modified kernels (Mokany et al., 2014a) (Figs S7 & S8), with slightly greater species richness (Fig. 3b) and compositional turnover (Fig. 4b). However, these differences could be tolerated if resources or knowledge restricted our ability to consider changes in dispersal capacity under climate change.

Not only does consideration of complex frugivore-mediated seed dispersal influence projected outcomes for plant biodiversity under climate change, it also changes the restoration management approach identified to be most beneficial in promoting biodiversity persistence into the future. For the focal region we assessed (the Atherton Tablelands) (Fig. S4), the configuration of restored habitat that best promoted biodiversity (the area of occurrence gained per species) changed from restoring habitat ‘corridors’ when the simple passive dispersal scenario was applied to restoring areas adjacent to ‘contiguous’ habitat when frugivore-mediated seed dispersal was considered (Table 1). Under the passive dispersal scenario there are fewer long-distance dispersal events than when frugivores are considered, resulting in fragmented habitat suffering a substantial loss of diversity (Fig. 3c) and benefiting markedly by connection to contiguous habitat through restoration corridors (Table 1). Habitat corridors are less relevant when the ability of frugivores to cross ‘matrix’ landscapes is considered (García et al., 2013), and instead the best outcomes for plant diversity are achieved through restoration adjacent to contiguous habitat (Table 1). These results demonstrate the potential importance of adequately considering key ecological processes when assessing alternative conservation management actions (Wintle et al., 2011; Mokany et al., 2013). Interestingly, an ad hoc ‘random’ approach to restoring habitat performed worst, or next to worst, for all dispersal scenarios (Table 1), emphasizing the value of strategic planning and assessment of conservation actions to achieve the best outcomes for biodiversity (Pressey et al., 2007; Moilanen & Wilson, 2009).

Although our study provides an unprecedented consideration of how complex dispersal processes influence outcomes for tropical forest biodiversity (all plant species), as with any modelling endeavour we have made a range of important assumptions and simplifications. For example, we have applied simple correlative modelling approaches to project frugivore abundances over space and time, ignoring potential limitations in frugivores shifting their distributions, as well as assuming no changes in frugivore movement behaviour or physiology under climate change (Mokany et al., 2014a). It is also possible that factors such as interspecific variation in fruit abundance, phenology and directionality of frugivore movement could influence outcomes in seed dispersal and plant community change. In addition, we have not considered direct feedbacks of projected change in plant community composition on frugivore abundances or foraging preferences, which may be expected through changes in habitat and the abundance of different fruit types (Kissling et al., 2008; Côrtes & Uriarte, 2013). In considering differences in the dispersal capacity of plant species we have ignored potential tradeoffs in terms of their competitive ability in community assembly (e.g. competition–colonization trade-offs; Calcagno et al., 2006). Finally, our analyses ignore the concomitant role of other potentially important drivers of biodiversity change, such as alien species invasions (Walther et al., 2009), altered fire regimes (Bowman et al., 2009) and further loss of habitat for human land use (Erskine, 2002). Although our study has not considered these factors, our main finding is clear: complex ecological processes, including the ones we have ignored, can be important in influencing the projection of biodiversity outcomes and identification of management priorities under climate change. The potentially strong influence of the ecological processes we have not considered therefore needs to be assessed in future modelling research.

In conclusion, we have demonstrated that complex frugivore-mediated dispersal processes make an important difference in the projection of outcomes for tropical plant biodiversity under climate change and the identification of the most effective management response. Although much attention has been given to predicting biodiversity outcomes under alternative climate scenarios (Beaumont et al., 2008), our results suggest that considering important ecological processes can be more important (Ockendon et al., 2014), and subsequently deserves greater modelling effort. The outcomes of ecological interactions and processes are often complex and difficult to model, yet our findings highlight the importance of accounting for such complexities if we are to improve our capacity to understand and respond to the influence of global change on biodiversity.

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REFERENCES


SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher’s web-site.

Figure S1 The study region: the Australian Wet Tropics.
Figure S2 The methodological framework applied to incorporate frugivore mediated dispersal into projected outcomes for plant biodiversity across the Australian Wet Tropics.
Figure S3 Conceptual illustration of the three dispersal scenarios applied.
Figure S4 The four restoration scenarios assessed for the Atherton Tablelands region of the Australian Wet Tropics.
Figure S5 The projected change in the area of occurrence for all species within each plant fruit group from 2010 to 2100, under the hot/dry climate scenario and ‘space and time’ dispersal scenario.
Figure S6 The projected net flux of species from 2010 to 2100 under the hot/wet climate change scenario.
Figure S7 The projected net flux of species from the ‘fig’ plant fruit group from 2010 to 2100 under the hot/dry climate change scenario.
Figure S8 The projected net flux of species from the ‘large drupe’ plant fruit group from 2010 to 2100 under the hot/dry climate change scenario.
Figure S9 The projected dissimilarity in the species composition of each grid cell from 2010 to 2100 under the hot/wet climate change scenario.
Figure S10 The projected compositional dissimilarity for each community from 2010 to 2100 under climate change, within each 100 m elevation category.
Figure S11 The projected net flux of species from 2010 to 2100 under climate change within each 100-m elevation category.

BIOSKETCHES

Karel Mokany specializes in developing, testing and applying novel macroecological modelling approaches to projecting outcomes for biodiversity under alternative scenarios of global change and management.

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