

Conservation benefits of international Aichi protection and restoration targets for future epiphyte metapopulations

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Abstract

1. More than half way towards the deadline for 2020 Aichi targets, a key question is whether the metapopulation dynamics of dispersal-restricted habitat specialists can be sustained under current international targets of protection and restoration.
2. We present the first metapopulation projections under scenarios of multiple Aichi biodiversity targets of protecting high-quality habitats and restoring suboptimal quality habitats under management. We simulate 200 years of metapopulation dynamics of nine old-growth beech (*Fagus sylvatica*)-associated epiphytic lichens, under a range of protection and restoration scenarios in a realistic landscape realm.
3. Protection was generally more efficient than restoration, where protection resulted in a constant increase in occupancy over time. However, projections showed that substantial increments in the number of occupied protected beech stands will most likely occur within the next 100–200 years. The time frame was dependent on species-specific dispersal restriction, occupancy levels at onset and forest-age requirements. Suboptimally restored beech stands increased lichen metapopulation sizes over a transient period and shortened the time for dispersal-restricted species to reach higher occupancy levels inside protected areas of the landscape (c. 85–125 years).
4. *Synthesis and applications.* Based on projections of metapopulation dynamics of species associated with old-growth forest, we argue that a combination of protection and restoration with the shortest possible time frame for increasing occupancy is the safest strategy. This is especially important under climatic and socio-political changes that are unforeseeable over centuries. If choosing between conservation strategies, highest priority should be given to increased protection because it means larger metapopulation sizes of these species on the long term.

KEYWORDS

Aichi, biodiversity targets, conservation planning, epiphytes, fragmentation, lichens, metapopulations, protected areas, restoration, scenario projections

1 | INTRODUCTION

To halt the loss of biodiversity and ecosystem services, the Convention on Biological Diversity (CBD) in 2010 adopted 20 “Aichi targets” to be met by 2020 (CBD, 2010). Aichi target 11 commits governments to protect $\geq 17\%$ of terrestrial environments, especially “areas of particular importance for biodiversity” through “ecologically representative”, “effectively and equitably managed”, and “well connected” protected area systems or other “area-based conservation measures” that are “integrated into the wider landscapes” (CBD, 2010). Setting aside land as protected areas has been the foundation of global efforts to conserve biodiversity (Rodrigues et al., 2004). About 14.6% of the planet’s terrestrial environment is formally protected; however, coverage targets for specific ecoregions, important sites for biodiversity or species are often substantially lower (Butchart et al., 2015).

While increasing protected areas is indeed one way of enhancing landscape connectivity (Hanski, 2011), they are not the sole solution for preserving species at regional scales (Margules & Pressey, 2000). Meeting national commitments of the multiple components of target 11 will require approaches of expanded protected area networks in addition to alternative conservation area approaches with more effective habitat management and prioritization (Butchart et al., 2015; Jonas, Barbuto, Jonas, Kothari, & Nelson, 2014). High-quality habitat in non-protected areas has been shown to improve landscape connectivity, the performance of protected areas and species persistence (Hodgson, Thomas, Wintle, & Moilanen, 2009; Margules & Pressey, 2000; Olds, Connolly, Pitt, & Maxwell, 2012; Pressey, Cabeza, Watts, Cowling, & Wilson, 2007). Given the vast extent and rate of ecosystem degradation world-wide, it is not surprising that the CBD also highlighted the need to restore at least 15% of degraded ecosystems by 2020 to improve habitat quality (Aichi Target 15; CBD, 2010). To date, restoration options for habitats, species and ecosystem services in accordance with target 15 have been given limited attention (Egoh, Paracchini, Zulian, Schägner, & Bidoglio, 2014; Tittensor et al., 2014).

Understanding how dispersal-restricted and habitat-specialist species respond to different protection and restoration targets is a particularly high priority, since they are less able to keep pace with the environmental changes inflicted by habitat loss and fragmentation. Epiphytic lichens are examples of such species, since their colonization is often restricted by diaspore output, dispersal range or establishment, while their extinctions are often caused by habitat destruction, i.e. treefall, or at stand scale, fall of the last occupied tree (Belinchón, Harrison, Mair, Várkonyi, & Snäll, 2017; Fedrowitz, Kuusinen, & Snäll, 2012; Gärdenfors, 2010; Johansson, Ranius, & Snäll, 2012; Snäll, Ehrlén, & Rydin, 2005). They are symbiotic associations between heterotrophic mycobionts (i.e. fungi) and autotrophic photobionts (green algae and/or cyanobacteria). Many crustose epiphytic lichens are slow-growing and long-lived organisms associated with high tree age (Fritz, Niklasson, & Churski, 2009), and their stochastic extinction rate from trees that remain standing is often negligible (e.g. Belinchón et al., 2017; Johansson et al., 2012 but see Öckinger & Nilsson, 2010; Fedrowitz et al., 2012). Hence, the time window when a forest constitutes a patch for epiphytes can be defined as the time between

when the forest obtains the required habitat quality (e.g. a minimum suitable age) and the time when it is clear-cut. There are intermediate successional stages in between, but we are not aware of any epiphyte colonization models accounting for these stages. Since this time window is narrow in managed forest landscapes, species with slow metapopulation dynamics are often lacking or declining in these landscapes (Dettki & Esseen, 2003; Fritz et al., 2009).

More than half way towards the 2020 Aichi targets, a key question is whether the metapopulation dynamics of dispersal-restricted habitat specialists can be sustained under current national and international Aichi targets of protection and restoration. Forecast studies of ecological dynamics and biological diversity are increasingly important tools for identifying conservation solutions in the changing world (Mouquet et al., 2015; Petchey et al., 2015).

In this study, we simulated the metapopulation dynamics of species with different dispersal properties, metapopulation sizes and stand age requirements to answer the question: is there a difference in response to alternative forest protection of high-quality habitats and restoration scenarios of suboptimal habitat under management on the future occupancy of epiphytic species? This involved testing responses to single as well as combined targets, compared to business-as-usual. We hypothesized that forest protection would increase future occupancy more than restoration, but that the relative importance of restoration would be significant for species with high colonization ability that do not only colonize very old stands.

2 | MATERIALS AND METHODS

We simulate 200 years of metapopulation dynamics of nine old-growth beech-associated epiphytic lichens with different dispersal capacities and stand age requirements, under a range of landscape-level protection and restoration scenarios in a realistic landscape realm.

2.1 | The study realm

We applied published epiphyte metapopulation dynamics models (Ruete, Fritz, & Snäll, 2014) to simulate the future metapopulation dynamics of the study lichens. These landscape-level metapopulation models were derived from thorough field inventories of 150 beech forest stands in a forest landscape located in southern Sweden (56°46′N 13°4′E), where current beech (*Fagus sylvatica*) forests represent 2% of the land cover of the landscape. The study landscape is situated in the transition zone between the nemoral and hemiboreal regions (Jonsell, 2004). Beech reached its maximum and dominant distribution in this region during early medieval times (Björkman, 1997). Historical maps have shown that less than 8% of the dominant beech forest area of the mid-1600s remains today. This decline in beech forest cover is the result of increased human exploitation; from transformations into heaths during the early 1900s (Malmström, 1939) to industrialized forestry at the end of the 1900s, with subsequent shifts in the forest composition towards dominance of planted Norway spruce (*Picea abies*). As much as 4.8% of the study landscape is currently protected,

including 10% of the current beech forest area. For further details on past changes, see Ruete et al. (2014).

Here we project the future occupancy of lichens in a realistic lattice landscape set-up to resemble the landscape in 1,650 in terms of the extent, connectivity and age distribution of protected and unprotected beech forest stands (see Figure S1a in Data S1). The total extent of the simulated lattice landscape was set equal to the approximate area of 718 km² of beech forest present in the mid-1600s as based on historical maps (Ruete et al., 2014), and was set up in 300 × 300 m grid squares. That is, we are simulating a total of 79 × 101 = 7,979 grid squares in a 23.7 × 30.3 km landscape. Because beech stands are typically smaller than spruce stands, we also aligned a finer resolution 150 × 150 m grid with the 300 × 300 m grid. Thereby, we could identify spruce-dominated 300 × 300 m grid squares and restore half or a quarter of them to beech forest. The whole lattice landscape comprised a total of 31,916 grid squares of 150 × 150 m. Beech squares were randomly allocated so that (1) the total beech cover area was not higher than 2%, (2) no more than two “beech squares” were selected per selected “spruce square” to reflect the size of the current beech stands and (3) in the latter case, these two squares share a side and not only a corner. Each beech grid square was assigned a random stand age drawn from the age distribution of the study landscape in Ruete et al. (2014), and was different for protected (mean = 161 years) and unprotected forest stands (mean = 82 years). The landscape configuration was simulated once and then species were projected onto that landscape based on their observed occupancy levels and species-specific suitable stand ages (Table 1). At onset, the landscape was composed of 1.8% ($n = 574$) unprotected and 0.2% ($n = 64$) protected beech squares (totally 14.4 km²), and 98% ($n = 31,278$) Norway spruce squares. For a detailed visual description of the landscape realm, see Figure S1a in Data S1.

2.2 | Simulation of epiphyte metapopulation dynamics and scenarios

The simulations were conducted using species-specific non-equilibrium lichen metapopulation models developed in Ruete et al. (2014). For five species, the models simulated spatially explicit colonizations determined by their force of colonization (which regulates the decadal rate of colonization resulting from dispersal from surrounding beech stands) and dispersal range (i.e. estimated as the exponentially decaying influence of the surrounding landscape with increasing distance). For the other four species, we could not find support for effect of distance, therefore the models simulated non-spatial colonizations, i.e. background colonization events determined by their force of colonization. For further model details, see Table 1 and Ruete et al. (2014). The Bayesian modelling approach applied here allows providing probabilistic support for differences in metapopulation size between the scenarios (Gelman & Hill, 2007). Using the models, we projected the future inter-decadal colonization and occupancy state of each species in each forest stands (i.e. grid squares) under nine scenarios of landscape protection and restoration configuration, where the protected area network was expanded and the spruce forest was restored to beech (Table 2). The metapopulation dynamics and forest stands were simulated over twenty 10-year time-steps where the forest patch ages increased accordingly. Unprotected beech forests were clear-cut at random ages with mean = 120 and SD = 5 years, to account for varying site conditions (Stefan Andersson, Swedish Forest Agency, pers. comm.). Clear-cut beech forests were assigned age 0 in the next time-step, but remained as beech forest, in accordance with the law. Local deterministic extinctions of the lichens were simulated for stands that were clear-cut. Stochastic extinction rates were

TABLE 1 Lichen study species, red list status (LC: least concern; NT: near threatened; VU: vulnerable; EN: endangered; ArtDatabanken, 2015), shortest spore dimension (μm) (Foucard, 2001; Smith et al., 2009), minimum suitable stand age, occupancy at the onset year 0, mean realized colonization rate per decade, force of colonization (a parameter regulating the decadal rate of colonization resulting from diaspore output from surrounding beech stands and establishment), and mean dispersal range of species with restricted dispersal range (names in bold). All species are epiphytic, except *Chaenotheca brachypoda* which is epixylic. The species nomenclature follows the Swedish Taxonomic Database (www.dyntaxa.se)

Species	Red list status	Minimum suitable stand age	Observed occupancy (onset; %)	Mean colonization rate (per decade) ^a	Force of colonization ^b	Mean dispersal range (m, rounded to nearest 100 m) ^c
<i>Bacidina phacodes</i>	NT	118	12	0.030	0.029	–
<i>Chaenotheca brachypoda</i> ^a	LC	118	11	0.025	0.51	1,800
<i>Gyalecta carneola</i>	VU	120	10	0.024	0.69	2,200
<i>Lecanora glabrata</i>	NT	86	35	0.058	1.51	1,200
<i>Megalaria laureri</i>	EN	120	9	0.028	0.028	–
<i>Pertusaria multipuncta</i>	NT	120	20	0.035	0.035	–
<i>Pyrenula nitida</i>	NT	86	43	0.075	3.09	4,700
<i>Thelopsis rubella</i>	VU	120	9	0.033	0.033	–
<i>Zwackhia viridis</i>	LC	113	12	0.025	0.38	200

^aMean of parameter η , eq. 2 in Ruete et al. (2014).

^bParameter φ , eq. 2 in Ruete et al. (2014).

^cParameter α^{-1} , eq. 3 in Ruete et al. (2014).

assumed to be negligible (zero) from uncut occupied beech stands (e.g. Belinchón et al., 2017; Johansson et al., 2012; Snäll et al., 2005). Species-specific connectivity measures to every suitable beech stand that could represent a potential dispersal source (based on species-specific minimum suitable stand age, see below) were calculated and ranked. Stochastic colonization events were simulated as a function of the calculated stand-specific colonization probabilities according to the species-specific models in Ruete et al. (2014) described in Table 1. To account for natural variation and uncertainty, we replicated each series of colonization events over 20 decadal time-steps (200 years) 200 times, each with a different set of parameter values drawn from the posterior probability distributions fitted in Ruete et al. (2014).

In the business-as-usual scenario, 10% of the beech forest was protected and there was no restoration of beech. For scenarios where the beech forest protection was expanded to 17%, we tested two approaches for selecting stands to be protected: (1) randomly choosing grid squares with beech and (2) choosing among grid squares with beech ranked according to their connectivity to protected areas. Hence, it was the additional 7% of beech forest and not the existing 10% that was assigned to be protected according to random or connectivity criteria. These protected squares were not clear-cut during the simulations. In restoration scenarios, randomly chosen 150 × 150 m spruce-dominated grid squares were restored into young beech forests (with random ages uniformly distributed between 0 and 30 years) until the beech forest cover reached 15% and 30% (Rest15 and Rest30 respectively). Restored forests were selected at random, to reflect an uncertainty concerning which of the many small landowners would agree to conduct restoration based on economic incentives offered by the government. After restoration, the percentage of protected area of the total beech forest cover ranged 0.7%–2% for the different scenarios (Table 2).

Occupancy levels were calculated as the number of occupied grid squares over the total number of grid squares with suitable beech forest, and were summarized for protected beech grid squares and all beech grid squares in the landscape. However, we emphasized the response inside protected areas since these provide the long-term protection. Conservationists and policy makers are particularly interested in future policy outcomes in relation to the business-as-usual scenario. Therefore, as a measure of the relative effect of different beech forest protection and restoration scenarios on the species occupancy, we calculated and plotted the chance that the simulated occupancy was greater (or lower) than the business-as-usual scenario (Prot10Rest0) at the future year 200. The chance is the probability that the difference in the number of occupied squares is larger than a defined increment level (e.g. a 20% increase). This probability is a point-estimate resulting from comparing the full predictive probability distributions that each scenario increased or decreased the metapopulation level compared to the business-as-usual scenario in year 200. For detailed information on the set-up of the simulations and the calculation of the chances for difference, see Data S1. We choose to depict the chance for a 20% increase in the main text, but the full range of probabilities for percentage change in the number of occupied protected beech stands are provided in Data S2. We considered a 20% increase in occupancy over

200 years as a minimum value for a successful development for rare species (see Table 1 for initial occupancies).

2.3 | The focal species

In this study, we simulate the metapopulation dynamics of nine epiphytic lichen species *Bacidina phacodes* (Körb.) Vězda, *Chaenotheca brachypoda* (Ach.) Tibell, *Gyalecta carneola* (Ach.) Hellb, *Lecanora glabrata* (Ach.) Malme, *Megalaria laureri* (Hepp ex Th.Fr.) Hafellner, *Pertusaria multipuncta* (Turner) Nyl., *Pyrenula nitida* (Weigel) Ach, *Thelopsis rubella* Nyl. and *Zwackhia viridis* (Ach.) Poetsch & Schied that are confined to a specific substrate (i.e. beech trees), but variable in term of forest-age requirements (Fritz et al., 2009) and colonization rates and ranges (Ruete et al., 2014). The species studied vary in metapopulation size (see Table 1 for the current occupancies), and the data allowed developing models for their metapopulation dynamics (Ruete et al., 2014). Based on Bayesian statistical modelling of empirical, observational data collected at the studied landscape scale, five species were found to be restricted by dispersal range, while four species were not found to have restricted dispersal range (Table 1; Ruete et al., 2014). The species specificity to old beech trees (Fritz et al., 2009) allowed us to assume that beech stands constitute the patches of the epiphytes' patch-tracking metapopulation dynamics (Belinchón et al., 2017; Johansson et al., 2012; Snäll, Ribeiro, & Rydin, 2003). The focal species are red-listed according to a range of IUCN threat categories (Table 2; ArtDatabanken, 2015) or indicator species of old-growth forests (Norén, Hultgren, Nitare, & Bergengren, 1995). Given the variety of ecological characteristics (i.e. forest-age requirements, dispersal ranges, metapopulation sizes and range of red list statuses) represented among these old-growth forest indicator species, they should be useful in gauging the effectiveness of direct forest conservation forest actions. They were assumed to be unable to colonize stands younger than the minimum stand age where each species were recorded (Table 1; Ruete et al., 2014). This minimum age determined the species-specific number of suitable habitat patches in the landscape. The species nomenclature follows the Swedish Taxonomic Database (www.dyntaxa.se, accessed on December 2015).

3 | RESULTS

The number of protected suitable beech stands occupied by these mainly red-listed species increased over time for all species under the business-as-usual scenario with 10% protection and no restoration (Prot10Rest0, Figure 1). However, the magnitude of the increase under this business-as-usual scenario was substantially lower than under the 17% protection target (Prot17RRest0) for all species except *G. carneola* (Figure 1). The scenario assuming the 15% restoration target (Prot10Rest15) only increased the number of protected stands occupied by three species that were restricted by dispersal range (Figure 1a). Furthermore, increasing restoration levels from 15% to 30% (Prot10Rest30) only had a substantial positive effect on *C.*

TABLE 2 Scenarios of protection and restoration under which the metapopulation dynamics of nine epiphytic lichen species were simulated in a 718-km² landscape

Scenario	Protection level (%)	Restoration level (%)	Total extent of beech (%)	% of beech forest protected	Description
Prot10Rest0	10	0	2	10	<i>Business-as-usual</i> : 10% beech forest protected and no restoration of beech
Prot10Rest15	10	15	15	1	<i>Aichi target 15</i> : 10% beech forest protected and 15% spruce forest restored to beech
Prot10Rest30	10	30	30	0.7	<i>Increased restoration</i> : 10% beech forest protected and 30% spruce forest restored to beech
Prot17RRest0	17	0	2	17	<i>Aichi target 11 without spatial prioritization</i> : 17% beech forest protected by randomly choosing grid squares with beech and no restoration of beech
Prot17RRest15	17	15	15	2	<i>Aichi target 11 without spatial prioritization and Target 15</i> : 17% beech forest protected by randomly choosing grid squares with beech and 15% spruce forest restored to beech
Prot17RRest30	17	30	30	1	<i>Aichi target 11 without spatial prioritization and increased restoration</i> : 17% beech forest protected by randomly choosing grid squares with beech and 30% spruce forest restored to beech
Prot17CRest0	17	0	2	17	<i>Aichi target 11 with spatial prioritization</i> : 17% beech forest protected by choosing beech grid squares based on ranked connectivity to protected stands and no restoration of beech
Prot17CRest15	17	15	15	2	<i>Aichi target 11 with spatial prioritization and Target 15</i> : 17% beech forest protected by choosing beech grid squares based on ranked connectivity to protected stands and 15% spruce forest restored to beech
Prot17CRest30	17	30	30	1	<i>Aichi target 11 with spatial prioritization and increased restoration</i> : 17% beech forest protected by choosing beech grid squares based on ranked connectivity to protected stands and 30% spruce forest restored to beech

brachypoda, *G. carneola* and *Z. viridis*, which were all restricted by dispersal range and had low occupancy levels (c. 10%) at the onset year 0 (Table 1). The scenario assuming the combined Aichi targets of 17% protection and 15% restoration (Prot17RRest15) increased the number of protected stands occupied by all species. However, expanding the protected area network was the most influential policy for increasing the metapopulation size of habitat specialists that started colonizing stands around 120 years old and for which there was no support for restricted dispersal range. Incorporating connectivity criteria in the selection of additional protected stands (Prot17CRest0-30) only had weak effects on the number of protected stands occupied by species that were restricted by dispersal range (Figure 1a).

The time needed for a substantial increase in the number of occupied protected suitable beech stands in the landscape was long under the 17% protection target (Prot17RRest0). Higher levels of occupancy of protected beech stands by species that were restricted by dispersal range

were achieved considerably faster when combining protection with restoration (e.g. Prot17RRest15) (Figure 1a). In fact, after 50–110 years, when the restored stands started to become suitable for colonization, there was a transient acceleration (i.e. steep slope) in the number of protected stands colonized per year. For species with restricted dispersal range (except *Z. viridis*), all protected stands were eventually colonized. The time needed to reach this state varied among individual species, between 85 and 125 years after restoration (Figure 1). As an example, the time needed to reach c. 40 occupied protected stands under the combined 17% protection and 15% restoration scenario (Prot17RRest15) ranged between 25 and 125 years for individual species that were restricted by dispersal range (Figure 1a), and 150–200 years for species that were not restricted by dispersal range and only colonizing old forest (Figure 1b). This variation in time depends on the species-specific age at which stands became suitable, occupancy level at the simulation start year 0, as well as the force of colonization and dispersal range (Table 1).

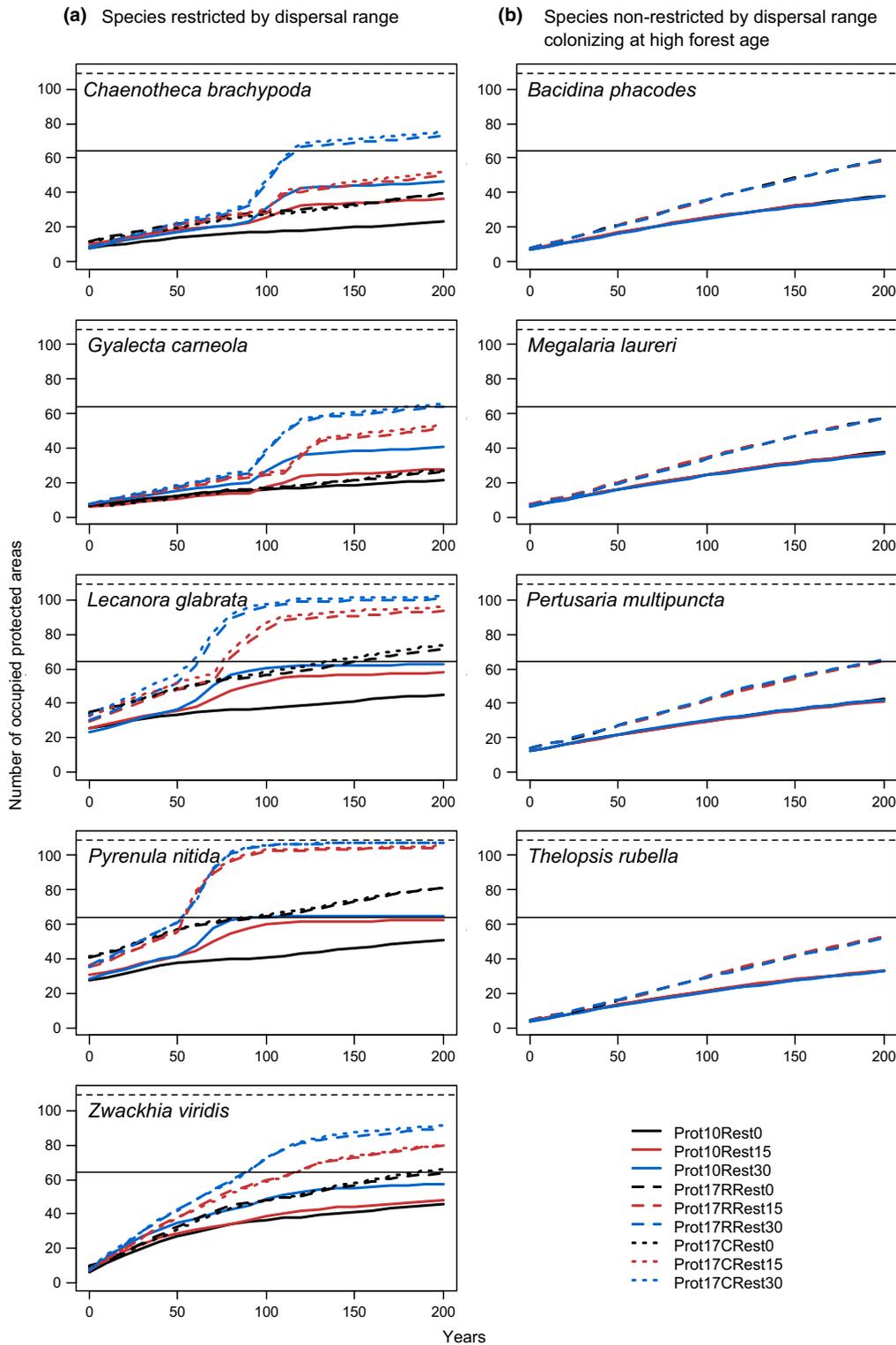


FIGURE 1 Mode of simulated number of protected suitable beech stands occupied by lichen species (a) restricted by dispersal range and (b) not restricted by dispersal range but colonizing at high forest age over the next 200 years. Nine scenarios of beech forest protection and restoration were simulated. Continuous and dashed horizontal lines show the number of protected areas in the Prot10 and Prot17 scenarios respectively

The transient increase in occupancy can be observed at the landscape level including protected and unprotected beech stands (Figure 2), where restored stands become occupied at different rates by different species after becoming suitable, and later unoccupied after clear-cutting after 120 (±5) years. There is a clear difference in

the magnitude of increase in occupancy between the two restoration scenarios (Rest15 and Rest30), but never do all restored stands become occupied. There are also differences explained by the force of colonization, dispersal range and the new landscape configuration. The number of occupied beech stands became particularly high for

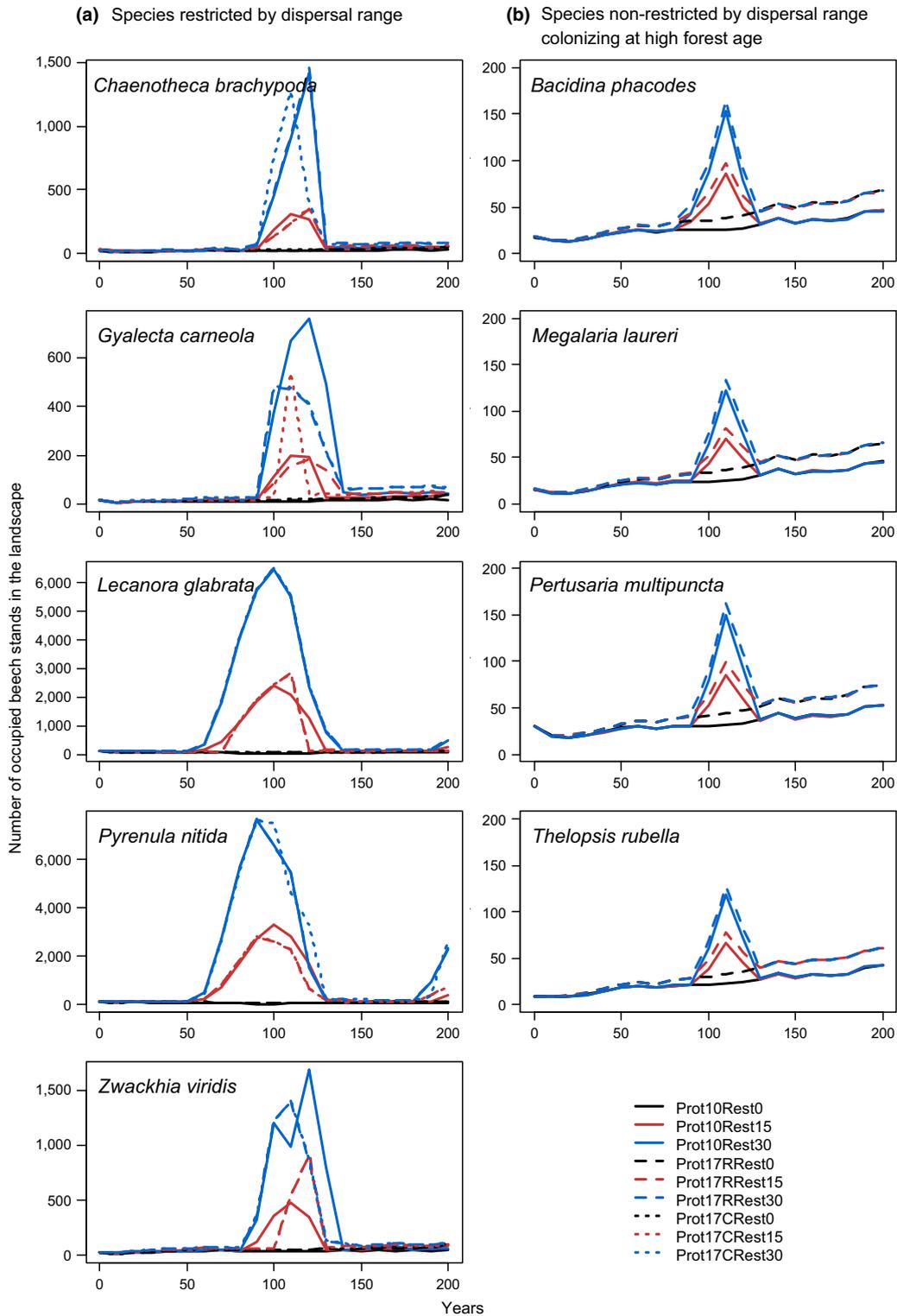


FIGURE 2 Mode of simulated total number of suitable beech stands in the study landscape occupied by lichen species (a) restricted by dispersal range and (b) not restricted by dispersal range but colonizing at high forest age over the next 200 years. Nine scenarios of beech forest protection and restoration were simulated

species with high forces of colonization and a minimum suitable stand age (Table 1) allowing them to colonize restored stands before they are cut, in accordance with our hypothesis. A second increase period starts to show at year 200 for the two species with lowest minimum

suitable stand ages when the earlier cut stands again become suitable for colonization. Of particular interest is the relatively short but high peak in number of occupied restored stands for *G. carneola* under scenario Prot17CRest15, where the configuration of the protected areas

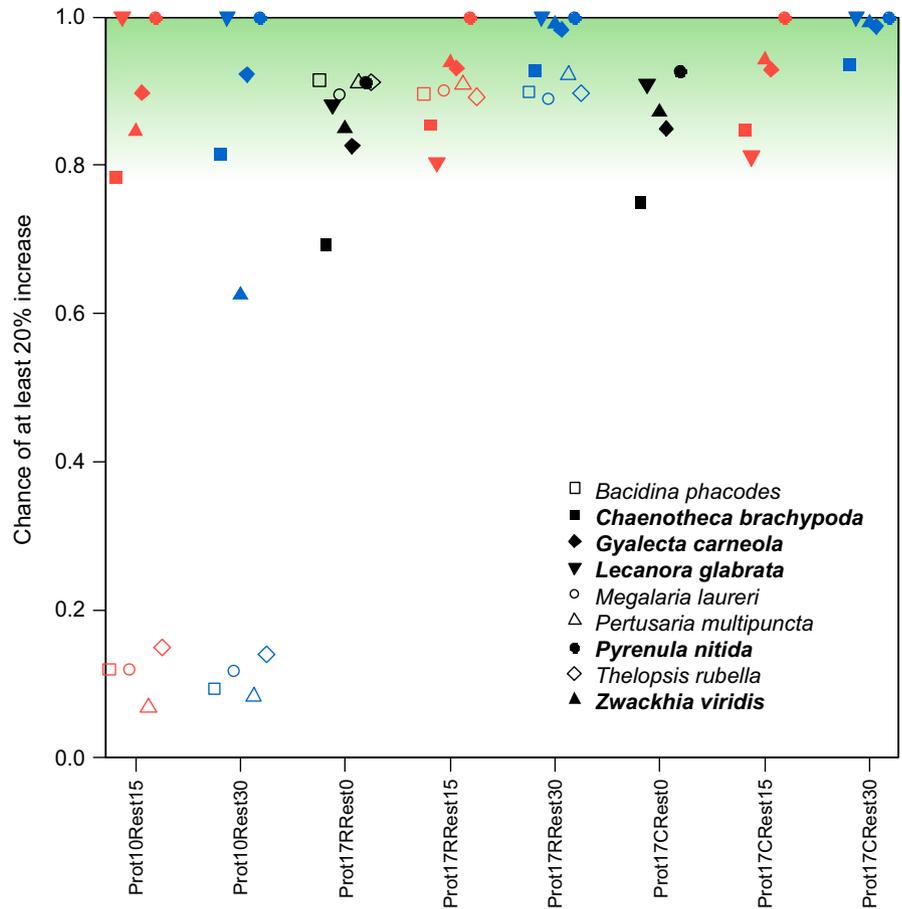


FIGURE 3 Chances of an increase in the number of occupied protected beech stands by each epiphytic species, of at least 20% by year 200, compared to the business-as-usual scenario (Prot10Rest0). Filled symbols and bold fonts show species that have restricted dispersal range and open symbols and regular font show species that were not shown to have restricted dispersal range and colonize old stands. Colours are a visual aid to discriminate between scenarios. A chance greater than 80% for an increase of at least 20% (marked with a green gradient) can be considered high. Chances are calculated comparing the full probability distributions of the projections by year 200

probably improved connectivity to a high number of beech stands that almost had the age of becoming suitable.

Only the combined scenarios of 17% protection and 15%–30% restoration could achieve a 20% increase for all species with a chance greater than 80% (Figure 3). Expanding the network of protected areas (Prot17RRest0) was generally more efficient than restoring degraded ecosystems (Prot10Rest15–30), but incorporating connectivity in the selection of protected beech stands did not have a strong influence on the chance of achieving a 20% increase in the number of occupied protected stands. The probabilities for a 20% increase in the number of occupied protected beech stands by year 200 applying combined scenarios of protection and restoration were overwhelmingly positive, and with minimal risks for negative changes for most species and scenarios (Data S2).

4 | DISCUSSION

We provide projections of conservation benefits for metapopulations of habitat-specialist species from implementing international Aichi biodiversity targets of increased protection and restoration. These are the first projections combining multiple conservation targets in a highly fragmented terrestrial ecosystem that we are aware of. A combination of both targets was the most effective and precautionary policy for promoting the metapopulations of epiphytic habitat specialists with a range of dispersal abilities and slow metapopulation

dynamics. Increased protection levels were generally more efficient than restoration. However, restoration shortened the time needed to reach high occupancy levels by temporally increasing the amount of habitat and therefore landscape connectivity (i.e. improved the green infrastructure) for the species that are able to colonize them before they are cut. Incorporating connectivity criteria in the protected area selection did not have a strong influence on the future metapopulation occupancies.

One prediction of metapopulation models with great importance for conservation is the time delay with which species are expected to track changes in the structure of fragmented landscapes (Hanski, 1998). As observed in Ruete et al. (2014), the species studied here are not at equilibrium with the landscape as their distribution pattern reflects the past rather than the current structure of the landscape. This explains our findings that species occupancies will keep increasing in the landscape in parallel to increasing beech forest age and areas (Figure 1). However, increasing the speed at which a more viable metapopulation level is reached is crucial given the current low levels after the habitat loss and fragmentation of beech forests in the landscape over the past centuries (Ruete et al., 2014). Our results illustrate that transient periods of increased availability of restored beech stands will shorten the time needed to obtain viable metapopulation sizes, after increasing the network of protected areas. Restored stands of suitable age may serve as transient local populations and stepping stones, i.e. a green infrastructure, for the colonization of protected stands during

a narrow time window before being clear-cut at a mean stand age of 120 years. For example, two species (*L. glabrata* and *P. nitida*) occupied almost all protected suitable grid squares after c. 100 years under combined protection and restoration scenarios (Prot17Rest15-30), but without restoration they would not reach these levels even after 200 years. Our findings agree with one earlier study where the low extinction rates of epiphytic lichens provided an opportunity to improve the future epiphyte metapopulation persistence through conservation actions ensuring improved tree regeneration over a period of around 100 years into the future (Johansson, Ranius, & Snäll, 2013). However, the studied lichen metapopulations mainly increased by improved tree regeneration in landscapes with high host tree densities at onset, especially for the species that mainly colonize very old trees (Johansson et al., 2013).

Perhaps counterintuitively, restoration did not affect the number of occupied protected areas by species not found to have restricted dispersal capacities. These results are likely due to a combination of these species' low force of colonization and high minimum suitable stand age (Table 1). The rate of establishment of epiphytes associated with old forest in sun-exposed (dry) conditions of young stands in managed landscapes has been shown to be low (Belinchón et al., 2017; Löbel & Rydin, 2009). Thus, the main limiting factor for increasing the metapopulation size of these species is the time the habitat is available and suitable for them to colonize.

The stand rotation times (i.e. patch longevities) will have a major influence on the viability of the studied epiphytic species in managed forest landscapes. The reason is that the species are affiliated with old forests (c. 120 years) and most of the beech forest stands are not present long enough to become colonized (Fritz et al., 2009). Increasing the rotation lengths of the restored stands will extend the length of the transient period when lichens such as *G. carneola*, *Megalania lauri*, *P. multipuncta* and *T. rubella* can build up their metapopulation size in the landscape. This may increase their metapopulation viability and also occupancy inside protected areas; but is something that remains to be studied. Recent experimental and empirical data have shown that the future metapopulation size of the lichen *Lobaria pulmonaria* is foremost set by the number of host trees located in shady uncut forest conditions, not isolated from occupied trees, and by the rotation length of these host trees (Belinchón et al., 2017). Increased rotation times of existing and restored stands above a mean clear-cut age of 120 years will likely also aid the implementation of national targets to increase the area cover of old forests (>120 years) in Sweden, although not by the target year 2020 (www.miljomal.se). Forestry activities can also be regulated with more and stronger complementary conservation strategies such as tree-retention measures, and these should also be incorporated as CBD targets (Lindenmayer et al., 2012). The future occupancy of our study species in the second generation of restored beech forest clear-cuts may have been underestimated by not accounting for tree-retention measures during clear-cutting.

Increased protection levels were important for the long-term protection of larger metapopulation sizes, which is important for ensuring higher metapopulation viability and lower impact of catastrophes and environmental variability in an uncertain future (Hanski & Ovaskainen,

2000; Ovaskainen, 2002). This is especially important given the unforeseeable climatic and socio-political changes that may become more influential in the future (Ellis, Klein Goldewijk, Siebert, Lightman, & Ramankutty, 2010). Moreover, as long as forecasts of biodiversity under climate change is in its infancy we cannot wait for it to develop in order to simulate and manage nature the best we can given current knowledge (Urban et al., 2016). This is particularly true for lesser studied organisms such as cryptogam species, for which we lack data on climate response, but still need to guide the effective protection of a large number of species (e.g. ArtDatabanken, 2015).

Expanding the network of protected areas resulted in a constant but slow future increase in occupancy for all species, except for *G. carneola* for which both increased protection and habitat restoration were required. Prioritizing the most connected beech forest stands for protection only resulted in a negligible further increase in occupancy for the three species with the shortest dispersal range *C. brachypoda*, *L. glabrata* and *Z. viridis*. In agreement with the habitat amount hypothesis (Fahrig, 1992, 2013) or the total patch area (Keymer, Marquet, Velasco-Hernández, & Levin Simon, 2000), these results indicate that the overall amount of suitable high-quality habitat is more important for the future occupancy than its spatial configuration in the landscape. Gjerde, Blom, Heegaard, and Sætersdal (2015) also showed that dispersal distances between forest fragments at the landscape scale may have small effects on the occurrence pattern of some epiphytic lichens. This is true at the current spatial configuration of the stands available for restoration and randomly choosing among them, but could be different if the locations to be restored could be chosen to prioritize landscape connectivity (Belinchón et al., 2017).

5 | CONCLUSIONS

Risks of ineffective outcomes from targets of increased protection (Butchart et al., 2015; Pouzols et al., 2014) and restoration (Egoh et al., 2014; Kotiaho, 2015) have been identified in response to land-use change, but never evaluated for future biodiversity. Our results assert that adoption and implementation of international Aichi biodiversity targets for increased landscape protection and restoration would contribute significantly to meeting the objectives of the CBD for halting the loss of biodiversity in fragmented terrestrial forest landscapes. To maximize conservation benefits, we advocate that approaches that simultaneously increase protection and restoration according to the levels of international biodiversity targets should be applied more broadly in conservation planning at the landscape scale. We suggest that approaches that combine the Aichi targets of 17% protection and 15% restoration for building up a green infrastructure should be implemented where feasible. If there is a choice, highest priority should be given to increased protection. Our results are likely relevant to many other epiphytic lichens, and also other sessile species in different organism groups that have restricted dispersal range and are dependent on tracking old-growth forest structures and habitat patches (Snäll et al., 2003). We contend that projections of future metapopulation dynamics is a powerful tool for identifying efficient

conservation solutions in a changing world that should be applied more broadly in conservation.

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AUTHORS' CONTRIBUTIONS

A.R., M.J. and T.S. conceived the ideas and designed methodology; A.R. run the simulations and analysed the data; A.R. and M.J. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All original data used to run the simulations in this manuscript are available in the Dryad Digital Repository <https://doi.org/10.5061/dryad.cg976> (Ruete et al., 2014).

REFERENCES

- ArtDatabanken. (2015). *Rödlistade arter i Sverige 2015*. Uppsala, Sweden: ArtDatabanken, SLU.
- Belinchón, R., Harrison, P. J., Mair, L., Várkonyi, G., & Snäll, T. (2017). Local epiphyte establishment and future metapopulation dynamics in landscapes with different spatiotemporal properties. *Ecology*, *98*, 741–750.
- Björkman, L. (1997). The history of Fagus forest in southwestern Sweden during the last 1500 years. *The Holocene*, *7*, 419–432.
- Butchart, S. H. M., Clarke, M., Smith, R. J., Sykes, R. E., Scharlemann, J. P. W., Harfoot, M., ... Burgess, N. D. (2015). Shortfalls and solutions for meeting national and global conservation area targets. *Conservation Letters*, *8*, 329–337.
- CBD (2010). Convention on Biological Diversity: Decision X/2: the strategic plan for biodiversity 2011-2020 and the Aichi biodiversity targets. Page 13 UNEP/CBD/COP/DEC/X/2.
- Dettki, H., & Esseen, P. A. (2003). Modelling long-term effects of forest management on epiphytic lichens in northern Sweden. *Forest Ecology and Management*, *175*, 223–238.
- Egoh, B. N., Paracchini, M. L., Zulian, G., Schägner, J. P., & Bidoglio, G. (2014). Exploring restoration options for habitats, species and ecosystem services in the European Union. *Journal of Applied Ecology*, *51*, 899–908.
- Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D., & Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography*, *19*, 589–606.
- Fahrig, L. (1992). Relative importance of spatial and temporal scales in a patchy environment. *Theoretical Population Biology*, *41*, 300–314.
- Fahrig, L. (2013). Rethinking patch size and isolation effects: The habitat amount hypothesis. *Journal of Biogeography*, *40*, 1649–1663.
- Fedrowitz, K., Kuusinen, M., & Snäll, T. (2012). Metapopulation dynamics and future persistence of epiphytic cyanolichens in a European boreal forest ecosystem. *Journal of Applied Ecology*, *49*, 493–502.
- Foucard, T. (2001). *Svenska skorplavor och svampar som växer på dem*. Stockholm: Interpublishing.
- Fritz, Ö., Niklasson, M., & Churski, M. (2009). Tree age is a key factor for the conservation of epiphytic lichens and bryophytes in beech forests. *Applied Vegetation Science*, *12*, 93–106.
- Gärdenfors, U. (2010). Rödlistade arter i Sverige 2010 – The 2010 red list of Swedish species. Swedish Species Information Centre in cooperation with Swedish Environmental Protection Agency, Uppsala, Sweden.
- Gelman, A., & Hill, J. (2007). *Data analysis using regression and multilevel/hierarchical models*. Cambridge, NY: Cambridge University Press.
- Gjerde, I., Blom, H. H., Heegaard, E., & Sætersdal, M. (2015). Lichen colonization patterns show minor effects of dispersal distance at landscape scale. *Ecography*, *38*, 939–948.
- Hanski, I. (1998). Metapopulation dynamics. *Nature*, *396*, 41–49.
- Hanski, I. (2011). Habitat loss, the dynamics of biodiversity, and a perspective on conservation. *Ambio*, *40*, 248–255.
- Hanski, I., & Ovaskainen, O. (2000). The metapopulation capacity of a fragmented landscape. *Nature*, *404*, 755–758.
- Hodgson, J. A., Thomas, C. D., Wintle, B. A., & Moilanen, A. (2009). Climate change, connectivity and conservation decision making: Back to basics. *Journal of Applied Ecology*, *46*, 964–969.
- Johansson, V., Ranius, T., & Snäll, T. (2012). Epiphyte metapopulation dynamics are explained by life-history, connectivity and patch dynamics. *Ecology*, *93*, 235–241.
- Johansson, V., Ranius, T., & Snäll, T. (2013). Epiphyte metapopulation persistence after drastic habitat decline and low tree regeneration: Time-lags and effects of conservation actions. *Journal of Applied Ecology*, *50*, 414–422.
- Jonas, H. D., Barbuto, V., Jonas, H. C., Kothari, A., & Nelson, F. (2014). New steps of change: Looking beyond protected areas to consider other effective area-based conservation measures. *Parks*, *20*, 111–128.
- Jonsell, B. (Ed.) (2004). *Flora Nordica. General Volume*. Stockholm: Bergius Foundation & Royal Swedish Academy of Sciences.
- Keymer, J. E., Marquet, P. A., Velasco-Hernández, J. X., & Levin Simon, A. (2000). Extinction thresholds and metapopulation persistence in dynamic landscapes. *The American Naturalist*, *156*, 478–494.
- Kotiaho, J. S. (2015). Finland: Target for ecosystem repair is impractical. *Nature*, *519*, 33.
- Lindenmayer, D. B., Franklin, J. F., Löhmus, A., Baker, S. C., Bauhus, J., Beese, W., ... Gustafsson, L. (2012). A major shift to the retention approach for forestry can help resolve some global forest sustainability issues. *Conservation Letters*, *5*, 421–431.
- Löbel, S., & Rydin, H. (2009). Dispersal and life history strategies in epiphyte metacommunities: Alternative solutions to survival in patchy, dynamic landscapes. *Oecologia*, *161*, 569–579.
- Malmström, C. (1939). Hallands skogar under de senaste 300 åren. *Meddelande från Statens Skogsförsöksanstalt*, *31*, 171–300.
- Margules, C. R., & Pressey, R. L. (2000). Systematic conservation planning. *Nature*, *405*, 243–253.
- Mouquet, N., Lagadeuc, Y., Devictor, V., Doyen, L., Duputié, A., Eveillard, D., ... Loreau, M. (2015). Predictive ecology in a changing world. *Journal of Applied Ecology*, *52*, 1293–1310.
- Norén, M., Hultgren, B., Nitare, J., & Bergengren, I. (1995). *Instruktion för datainsamling vid inventering av Nykelbiotoper*. Jönköping, Sweden: National Board of Forestry.
- Öckinger, E., & Nilsson, S. G. (2010). Local population extinction and vitality of an epiphytic lichen in fragmented old-growth forest. *Ecology*, *91*, 2100–2109.
- Olds, A. D., Connolly, R. M., Pitt, K. A., & Maxwell, P. S. (2012). Habitat connectivity improves reserve performance. *Conservation Letters*, *5*, 56–63.
- Ovaskainen, O. (2002). Long-term persistence of species and the SLOSS problem. *Journal of Theoretical Biology*, *218*, 419–433.

- Petchey, O. L., Pontarp, M., Massie, T. M., Kéfi, S., Ozgul, A., Weilenmann, M., ... Pearce, L.S. (2015). The ecological forecast horizon, and examples of its uses and determinants. *Ecology Letters*, *18*, 597–611.
- Pouzols, F. M., Toivonen, T., Di Minin, E., Kukkala, A. S., Kullberg, P., Kuusterä, J., ... Moilanen, A. (2014). Global protected area expansion is compromised by projected land-use and parochialism. *Nature*, *516*, 383–386.
- Pressey, R. L., Cabeza, M., Watts, M. E., Cowling, R. M., & Wilson, K. A. (2007). Conservation planning in a changing world. *Trends in Ecology & Evolution*, *22*, 583–592.
- Rodrigues, A. S. L., Andelman, S. J., Bakarr, M. I., Boitani, L., Brooks, T. M., Cowling, R. M., ... Yan, X. (2004). Effectiveness of the global protected area network in representing species diversity. *Nature*, *428*, 640–643.
- Ruete, A., Fritz, Ö., & Snäll, T. (2014). Data from: A model for non-equilibrium metapopulation dynamics utilizing data on species occupancy, patch ages and landscape history. *Journal of Ecology*, *102*, 678–689. <https://doi.org/10.5061/dryad.cg976>
- Smith, C. W., Aptroot, A., Coppins, B., Fletcher, A., Gilbert, O., James, P., & Wolsele, P. (Eds.) (2009). *The Lichens of Great Britain and Ireland*, (2nd edn). London: British Lichen Society.
- Snäll, T., Ehrlén, J., & Rydin, H. (2005). Colonization-extinction dynamics of an epiphyte metapopulation in a dynamic landscape. *Ecology*, *86*, 106–115.
- Snäll, T., Ribeiro, P. J., & Rydin, H. (2003). Spatial occurrence and colonisations in patch-tracking metapopulations: Local conditions versus dispersal. *Oikos*, *103*, 566–578.
- Tittensor, D. P., Walpole, M., Hill, S. L. L., Boyce, D. G., Britten, G. L., Burgess, N. D., ... Ye, Y. (2014). A mid-term analysis of progress toward international biodiversity targets. *Science*, *346*, 241–244.
- Urban, M. C., Bocedi, G., Hendry, A. P., Mhoub, J.-B., Pe'er, G., Singer, A., ... Travis, J. M. J. (2016). Improving the forecast for biodiversity under climate change. *Science*, *353*, aad8466.

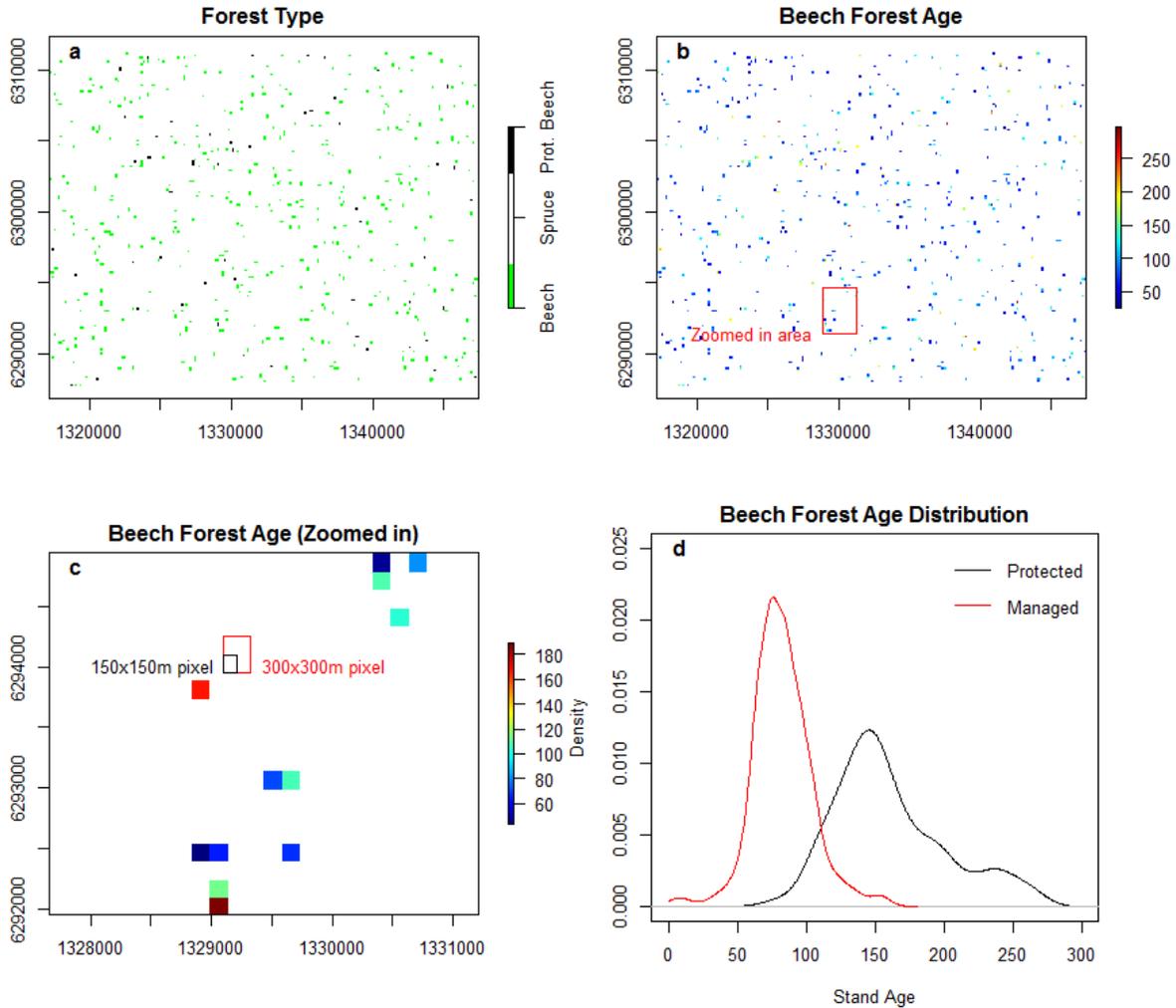
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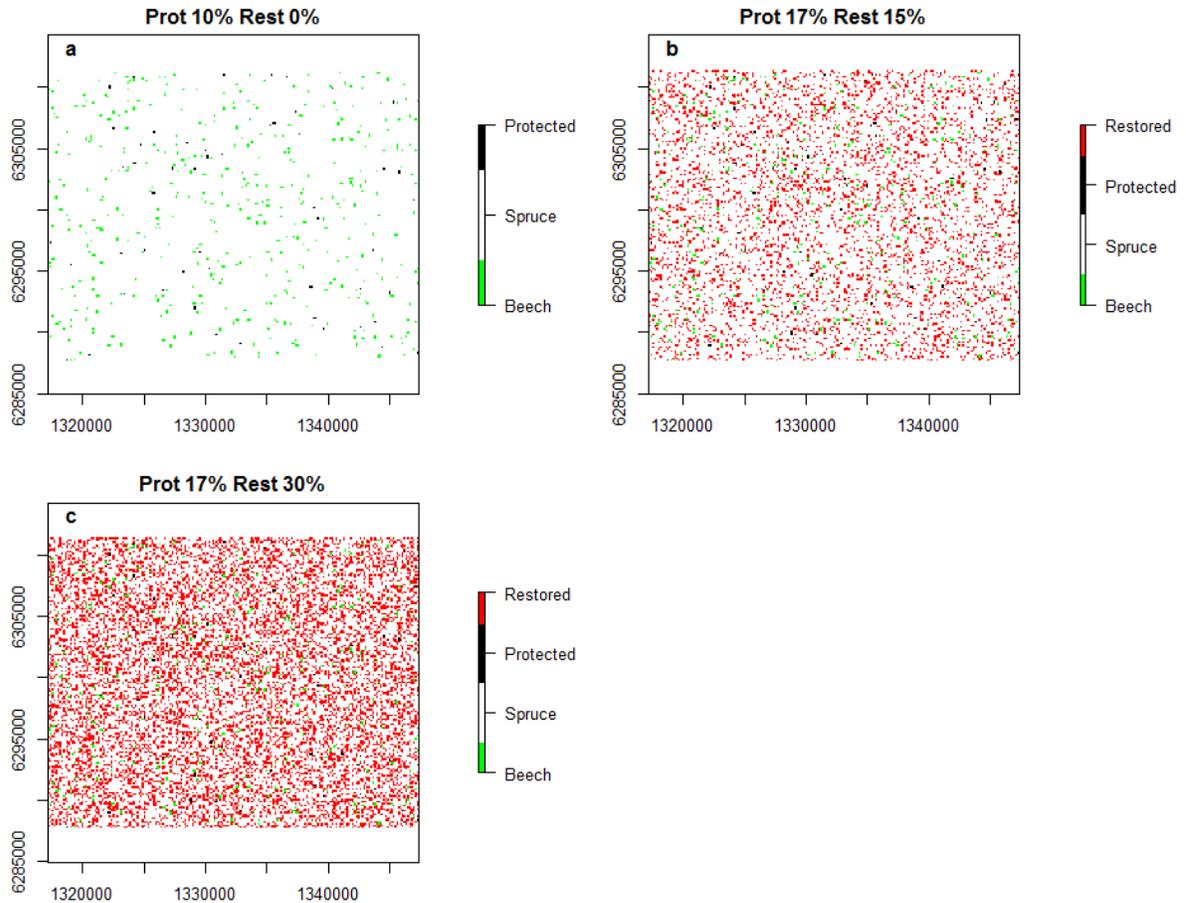
Conservation benefits of international Aichi protection and restoration targets for future epiphyte metapopulations. *J Appl Ecol*. 2018;55:118–128. <https://doi.org/10.1111/1365-2664.12964>

1 **Supplementary information S1: The simulated landscape realm and simulation procedure**
2
3 **Figures describing the simulated landscape realm**



4
5 **Figure S1a.** Map of (a) forest types and (b) beech forest age distribution (years) in the simulated
6 landscape realm. (c) Zoomed in area showing the 300 x 300 m grid squares for spruce and finer
7 resolution 150 x 150 m squares for beech, as well as the forest age of beech in the zoomed in
8 area (b). (d) The beech forest age distribution in protected areas and managed forests.

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13 **Figure S1b.** Map of forest types at year 200 in (a) the business-as-usual scenario of 10%
14 protection and no restoration, (b) the Aichi biodiversity targets of 17% protection and 15%
15 restoration, and (c) the 17% protection and expanded 30% restoration scenarios.

16

17 **Simulations of epiphyte metapopulation dynamics**

18 Simulations were based on a spatially explicit non-equilibrium metapopulation model fitted
19 using Bayesian inference (Ruete et al. 2014). This model allowed us to simulate the future
20 colonization process and occupancy under nine different scenarios of landscape protection and
21 restoration configuration, where protection levels were increased and the spruce forest was
22 restored to beech (Table 1 in main text). The simulations were run in R v3.2 (R Core Team 2015)
23 using 200 randomly sampled sets of parameter estimates from the posterior probability
24 distribution (PPD) of all parameters estimated in Ruete et al (2014). Stand-specific
25 environmental variables such as stand area, slope (%), aspect (degrees from south), and soil

26 productivity did not explain the colonization probability of any of the nine lichens in Ruete et al.
27 (2014), and were therefore did not included in the current simulations. Occupancy levels were
28 calculated as the number of occupied grid squares over the total number of grid squares with
29 suitable beech forest (i.e., 300 x 300 m grid squares with at least 50% cover of suitable beech
30 forest) and were summarized for protected suitable beech grid squares and for all suitable beech
31 grid squares in the whole landscape.

32
33 In the business-as-usual scenario 10% of the beech forest was protected and there was no
34 restoration of beech (Fig. S1b). For scenarios where the beech forest protection was expanded to
35 17% we tested two approaches for selecting protected stands: a) randomly choosing grid squares
36 with beech and b) choosing among grid squares with beech ranked according to their
37 connectivity to established protected areas. These protected squares were not clear-cut during the
38 simulations. In restoration scenarios, randomly picked 150 x 150 m spruce-dominated grid
39 squares were restored into young beech forests (with random ages uniformly distributed between
40 0-30 years) until the beech forest cover reached 15 and 30% (Rest15 and Rest30, respectively).
41 After restoration, the percentage of protected area of the total beech forest cover ranged between
42 0.7-2% for the different scenarios. Forest stand ages were simulated during twenty 10-year time-
43 steps with ages increased accordingly. Unprotected beech forests were clear-cut at random ages
44 with mean = 120 and SD = 5 years, simulating variability in site conditions (Stefan Andersson,
45 Swedish Forest Agency, pers. comm.). Clear-cut forests were assigned age 0 in the next time
46 step. Forest composition did not change after clear-cutting.

47
48 Metapopulation simulations were run for all species in all nine scenarios, where species-specific
49 connectivity measures to every suitable beech stand (based on species-specific minimum suitable
50 stand age, see below) that could represent a potential dispersal source was calculated and ranked.
51 Stochastic colonization events were simulated taking into account the estimated stand specific
52 colonization probabilities according to Ruete et al. (2014). Deterministic extinctions were
53 simulated for stands that were clear-cut. Stochastic extinction rates were assumed to be
54 negligible from uncut occupied beech stands (e.g. Snäll, Ehrlén & Rydin 2005; Johansson,
55 Ranius & Snäll 2012; Ruete et al. 2014; Belinchón et al. 2017).

56

57 As a measure of the relative effect of different beech-forest protection and restoration scenarios
 58 on the species occupancy, we calculated the chance that the simulated occupancy was greater
 59 than the Prot10Rest0 baseline scenario at the future year 200. This was conducted for each
 60 scenario based on the posterior probability distribution (PPD) of the scenarios. That is, we
 61 calculated the probability that each scenario increased or decreased the metapopulation level
 62 compared to the business-as-usual scenario. To do this we first defined the change as

$$\Delta Scn_r = \frac{NScn_r - NR_r}{NR_r} \cdot 100$$

63 where $NScn_r$ is a random sample r from the PPD for number of occupied beech stands in a focal
 64 scenario, and NR_r is a random sample r from the PPD for number of occupied beech stands in
 65 the business-as-usual scenario (reference level). A large enough number of random samples, i.e.
 66 $r = 10\,000$, was drawn from each PPD to ensure full comparison of both probability
 67 distributions. Then, assuming an increment level of $X\%$ we defined the variable $IncX_r$ for each
 68 scenario as

$$IncX_r = \begin{cases} 1, & \Delta Scn_r \geq X \\ 0, & \text{otherwise} \end{cases}$$

69 Where $X \in \mathbb{R}^+$. The probability of increment $P(IncX)$ is then

$$71 \quad P(IncX) = \frac{\sum_{r=1}^{10000} IncX_r}{10000}$$

72 For decrements $X \in \mathbb{R}^-_{\geq -100}$ and the condition for $DecX_r = 1$ was $\Delta Scn_r \leq X$.

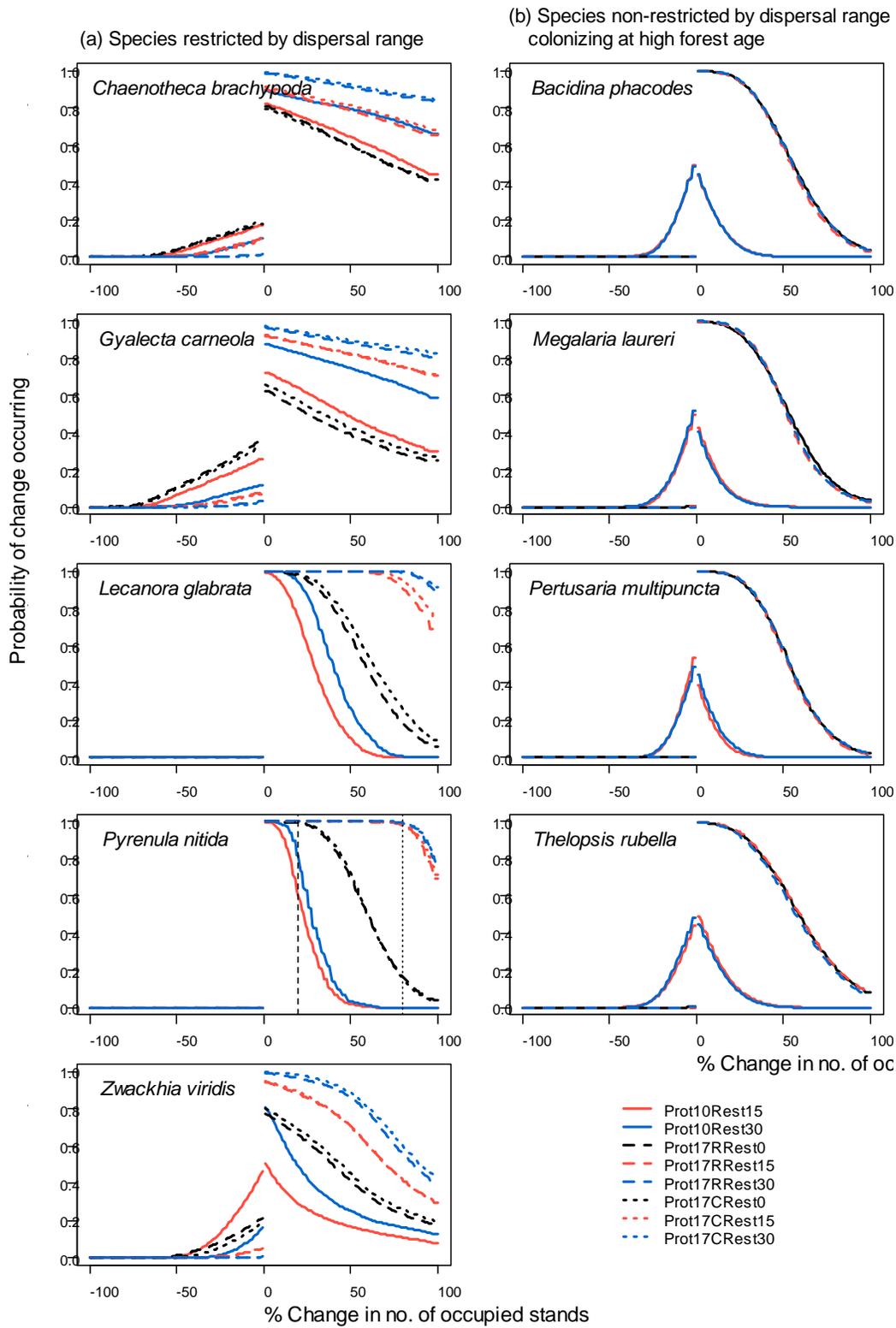
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75 **References cited**

- 76 Belinchón, R., Harrison, P.J., Mair, L., Várkonyi, G. & Snäll, T. (2017) Local epiphyte
 77 establishment and future metapopulation dynamics in landscapes with different spatiotemporal
 78 properties. *Ecology*, **98**, 741–750.
- 79 Johansson V, Ranius T, Snäll T. 2012. Epiphyte metapopulation dynamics are explained by life-
 80 history, connectivity and patch dynamics. *Ecology* **93**:235–241
- 81 Ruete A, Fritz Ö & Snäll T. 2014. A model for non-equilibrium metapopulation dynamics
 82 utilizing data on species occupancy, patch ages and landscape history. *Journal of Ecology*
 83 102:678–689

84 R Core Team (2015). R: A language and environment for statistical computing. R Foundation for
85 Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
86 Snäll T, Ehrlén J, Rydin H. 2005. Colonization-extinction dynamics of an epiphyte
87 metapopulation in a dynamic landscape. *Ecology* **86**:106–115.
88

1 **Supplementary Information S2: Chances for percentage changes in the number of**
 2 **occupied protected beech stands**



3

4 **Figure S2.** Projected chances for a negative or positive percentage change in the number of
5 protected suitable beech stands occupied by lichen species (a) restricted by dispersal range and
6 (b) not restricted by dispersal range but colonizing at high forest age by year 200. The
7 projections assumed eight beech forest protection and restoration scenarios, in relation to the
8 baseline scenario. For example, the chance for the number of protected stands occupied by
9 *Pyrenula nitida* to increase by at least 20% (x-axis) is 60-100% under any of the scenarios with
10 restoration (vertical dashed line). Moreover, there is a 100% chance for an increase with 80% in
11 the number of occupied protected stands in scenarios with both protection and restoration
12 (vertical dotted line). For 17% protection and no restoration (black lines), this chance is only
13 about 15%. The apparent negative growth of some scenario combinations compared to the
14 business as usual scenario is actually the expected distribution of probabilities when comparing
15 point-to-point (observation to observation) of two independent distributions that overlap almost
16 perfectly (See overlapping lines in Figs. 1 and 2). This shows for example that the probability of
17 decreasing by <1% is lower or equal to 0.50, and equal to the chance of increasing by 1%. That
18 is, the confidence intervals overlap almost completely.