Received: 19 August 2024 | Revised: 31 January 2025 | Accepted: 31 March 2025

DOI: 10.1002/eap.70041

ARTICLE

ECOLOGICAL APPLICATIONS
ECOLOGICAL SOCIETY OF AMERICA

National-scale mapping of potential floral resources for honeybees and native pollinators in New Zealand

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Funding information
Ministry for Business, Innovation and Employment, Grant/Award Number: C09X1608

Handling Editor: Luc Barbaro

Abstract

Floral resources are important food resources for pollinators. These resources are produced in different quantities depending on land cover and plant species composition, and the quantity of production varies seasonally. As such, land use change and management of natural resources can have substantial impacts on conservation through resource provision for pollinators, and also commercial enterprises through resources for honeybee hives which require adequate forage to be successful. In New Zealand, locations with vegetation that produce high-value honey also suffer from overcrowding of hives, as beekeepers compete for this valuable resource. At present, there is a lack of quantitative spatial data describing the production of these resources, especially over large spatial scales. Here, using maps of land cover and environment, and a large vegetation plot dataset, we show that the provision of floral resources for pollinators can be estimated spatially at national scales. These maps can be used to estimate the consequences of changing land cover, both historical and with future management actions, and to understand potential threats to floral resource provision. We find that the production of floral resources across New Zealand is highly seasonal, and overwhelmingly produced by indigenous land cover types, especially within public conservation land. Within forests, we show that floral production is dominated by a small number of plant families. Our results show the importance of native land cover for the provision of floral resources for commercial honeybee enterprises and also native pollinators. We anticipate our results will be a starting point to inform management decisions regarding the placement and stocking density of honeybee hives, and also the concession process for honeybee permits on public land. We also show how the restoration of woody ecosystems on cleared land can benefit the conservation of native pollinators by providing abundant and high-quality forage across all seasons.

KEYWORDS
apiculture, *Apis mellifera*, flowering phenology, honey production, honeydew, mānuka honey, national scale, nectar production, pollen production, pollination, seasonality, spatial variation

INTRODUCTION

Honeybees (*Apis mellifera*) and other pollinators primarily consume nectar from flowers which is produced by the plant as a reward for pollination, as it has a very high sugar content. Sugars are also collected by honeybees as honeydew which is excreted by sap-feeding aphids and scale insects (Beggs et al., 2005). After consumption to meet daily energetic needs, honeybees are left with a surplus of nectar of around 30% which is stored as honey (Southwick & Pimentel, 1981). Honeybees also consume pollen that provides proteins, lipids, vitamins, and minerals for development of the hive and brood rearing (Brodschneider & Crailsheim, 2010). Rates of honey production vary seasonally according to flowering phenology, honeydew production, and temperature, as hive activity is strongly limited below c. 10°C (Heinrich, 1979). Hive placement also influences honey production with much greater yields in locations with high densities of nectar-laden plants. Commonly, these areas are associated with commercial crops (Southwick & Pimentel, 1981), but also include urban areas (Matsuzawa & Kohsaka, 2021) and natural communities rich in plants that produce high volumes of nectar and honeydew (Butz Huryn, 1995; Moller & Tilley, 1989).

There are at least 40 species of bee (Hymenoptera, Apoidea) in New Zealand, 13 of which have arrived since European settlement (c. 1840) with eight of these introduced to aid crop pollination (Donovan, 2007; Howlett & Donovan, 2010). The first documented introduction of honeybees to New Zealand was in 1839 (Hopkins, 1911) and these generalist pollinators are now present as managed hives throughout the country (Donovan, 2007). The honeybee is the most reliable and cost-effective pollinator of New Zealand crops (Howlett & Donovan, 2010) contributing an estimated NZ$5 billion to GDP (Newstrom-Lloyd, 2013). New Zealand's native flora has a high proportion of species with unspecialized small flowers well suited to generalist pollinators like the honeybee (Butz Huryn, 1995; Lloyd, 1985). Feral colonies were once common in New Zealand forests and shrublands, but they have become scarce since the arrival of the varroa mite (*Varroa destructor*) in 2000 (Hall et al., 2021). As such, visitation of native vegetation by honeybees is now primarily restricted to managed hives.

The annual rate of honey production has been increasing globally with a 41% increase between 2000 and 2021 (Food and Agriculture Organization of the United Nations, 2022), and also in New Zealand (a 53% increase between 2014 and 2020; Ministry for Primary Industries, 2020). In 2022/2023 honey exports were worth NZ$379 million to the New Zealand economy, largely driven by high-value monofloral mānuka (*Leptospermum scoparium*) honey (Ministry for Primary Industries, 2023) which is promoted for its medicinal and antibacterial properties (Allen et al., 1991). Mānuka is a small tree that favors waterlogged or low-fertility soils, and naturally disturbed sites, such as landslides and fire-prone heathlands (Stephens et al., 2005). Anthropogenic disturbance since human arrival in the 13th century has favored mānuka (Perry et al., 2014), particularly in recent decades with the abandonment of former agricultural lands where it can dominate and act as a nurse species facilitating forest regeneration (Burrows, 1973). These areas now produce high-value mānuka honey. Honey from other New Zealand native plants is also targeted by beekeepers, and New Zealand exports over 2000 t of honey from other species (Ministry for Primary Industries, 2020) which includes non-natives like clover (*Trifolium* spp.), bugloss (*Echium vulgare*), thyme (*Thymus vulgaris*) and other pastoral weeds. Important native sources include kāmahi (*Pterophylla racemosa*), rātā (*Metrosideros* spp.), rewarewa (*Knightia excelsa*), kānuka (*Kunzea ericoides*) and honeydew produced by scale insects in some beech (*Fuscospora* spp.) forests (Ministry for Primary Industries, 2020; Moar, 1985). Māori landowners are major producers of mānuka honey (Harcourt et al., 2022) as much Māori land is undeveloped and has a high proportion of indigenous shrubland suitable for honey production (Ministry for the Environment & Stats NZ, 2018).

There has been an exponential growth in hive, beekeeper, and apiary numbers in New Zealand over the past c. 20 years (Newstrom-Lloyd, 2015, 2016). Unprecedented demand on both native and non-native floral resources in many regions has raised concerns that demand may outstrip supply, leading to poor honeybee health, excessive competition with native pollinators, and maintenance of hives with artificial supplements (Newstrom-Lloyd, 2016). Land use change has greatly affected floral resources (Newstrom-Lloyd, 2013). Many commercial beekeepers rely on concessions to mānuka shrublands and forests on public conservation land, creating poorly understood competitive risks to native pollinators (Beard, 2015). The expansion and intensification of dairy farming in New Zealand over the past three decades (Foote et al., 2015), often replacing less intensive sheep and beef farming (Norton et al., 2020), are also affecting floral resources, as intensively managed grasslands have few nectar-producing plants (Ausseil et al., 2018). In order to manage hive numbers, stocking densities, and placement sustainably, it is thus critical to understand the availability of floral resources at a landscape scale.

Quantifying the spatial supply of floral resources across land use types is difficult due to the large diversity of nectar-producing species, each with a different distribution, abundance, flowering phenology, and yield. Globally, there have been a few attempts to quantify spatial patterns of floral resource production. Woinarski et al. (2000) and Hawkins et al. (2018) used vegetation maps and flowering patterns to produce nectar production maps in regions of Australia to quantify nectar availability for birds. A map of nectar production for much of the western United States was used to predict hummingbird abundances (Feldman & McGill, 2014). Detailed measures of nectar production at the flower level, and data on species composition across vegetation types over two time periods, were used to map the decline of nectar supply in Britain (Baude et al., 2016). Specific to honeybees, models have been used to understand the carrying capacity of hives (Al-Ghamdi et al., 2016; Wakjira & Gela, 2019) and the impact of spatial configuration (Henry et al., 2012). Agent-based foraging models are also available, simulating colony dynamics by accounting for foraging activities, scouting activities, resource constraints, and stressors like varroa mite and pesticides (Becher et al., 2016). Affek (2018) produced an annualized honey production map for an 812 km^2 area of northeast Poland using vegetation data and expert opinion. Maps have also been produced for monthly nectar and pollen production and supply in a similar-sized catchment in the North Island of New Zealand (Ausseil et al., 2018). This example included a scenario highlighting the benefit of restoring riparian areas for the provision of floral resources. Other studies have produced maps indicating sites as suitable or unsuitable for keeping honeybees (e.g., Abou-Shaara et al., 2013; Gallant et al., 2014; Zoccali et al., 2017), but there have been no attempts to quantify the level of floral resources at a national scale.

In this paper, we create monthly maps of sugar (nectar and honeydew) and pollen availability to honeybees across all of New Zealand. From these, we derive spatial supply maps, incorporating the foraging activity of honeybees, that predict the resource available to an apiary at any location. We also assess the impact on floral resources of forest clearing since European settlement in the 19th century. We then compare results for different land cover and use to highlight their individual contributions to honey production. In particular, we show results comparing contemporary indigenous versus non-indigenous cover, public conservation land versus other, Māori land versus other, and two major pastoral farming systems in New Zealand (dairy farming and sheep and beef farming).

METHODS

Floral resource production maps

We produced monthly maps estimating potential nectar production per unit area and potential pollen production per unit area (both in kilograms per hectare per year) for honeybees across the mainland and surrounding inshore islands of New Zealand. These maps are based on two spatial land characterization products: the New Zealand Land Cover Database (LCDB) Version 5.0 (Manaaki Whenua – Landcare Research, 2020) and the Land Environments of New Zealand (LENZ) Level II, which is a national environmental classification (Leathwick et al., 2002).

The LCDB is a polygon-based map of land cover types that divides New Zealand into 33 classes, each of which includes vegetation consisting of plant species that produce different levels of nectar and pollen. Estimates of floral resource available in each land cover type depend on the composition of these plant communities, and the species-level quality and quantity of floral resource over the course of the year (Crane, 1975; Hicks et al., 2016). Ideally, estimates of floral resource production would be obtained for all plant species then summed across plant communities and land cover types (see Baude et al., 2016; Hicks et al., 2016). While these data are available for some New Zealand plant species (e.g., mānuka; Clearwater et al., 2021; Noe et al., 2019), this is nowhere near complete enough to produce national maps for a New Zealand higher plant flora comprising 2167 native (Schönberger et al., 2020) and >21,000 non-native (M. Dawson, personal communication, 3 February 2023) species. In a recent study, Ausseil et al. (2018) used the LCDB to estimate nectar and pollen production, hive-level resource supply, and landscape hive carrying capacity in the upper catchment of the Ruamahanga River in the North Island (83,000 ha). They used species-level floral resource values (where available), scaled up to the land cover category based on the proportion of the land cover occupied by the species, also incorporating a value for pollen quality. Monthly values of nectar and pollen production were estimated from annual production by distributing the annual total through the months when flowering occurs based on field observation, literature review, and expert knowledge.

We built on this approach, extending it to cover all of New Zealand and to incorporate species compositional variation across environments within each native land cover type. We applied the same nectar, pollen, and phenology values for the 11 LENZ classes from their study region and derived values for the remaining classes by following their methodology or by applying values from their most similar class (Appendix S1: Sections S1 and S2). Several largely non-vegetated classes—e.g. Permanent Snow and Ice, River—were assumed to have no (or negligible) floral resources. For the native woody classes—Broadleaved Indigenous Hardwoods, Indigenous Forest, Mānuka and/or Kānuka, Matagouri or Gray Scrub, and Sub Alpine Shrubland—we used a new approach to account for the broad range of vegetation types that vary widely across the country.

For example, the Indigenous Forest class includes forest types ranging from extensive areas of monospecific beech forest in drier montane regions, through to species-rich admixtures of beech, broadleaf, and conifer forests in oceanic, lowland, and northern regions (Wardle, 1991). For all native woody classes, we intersected LCDB with LENZ Level II, which is a raster-based classification of New Zealand's environment using climate, landform, and soil variables chosen for their roles in driving spatial variation of vegetation types (Leathwick et al., 2002). LENZ was generated at four levels of detail containing from 20 (Level I) to 500 (Level IV) environments, with environments from higher levels nested hierarchically within environments from lower levels, from which we used Level II (100 environments). To generate assemblages for each LENZ Level II environment, we obtained relevé data for 7308 vegetation plots (Appendix S1: Section S3) from the New Zealand National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz). Plots were 400 m^2 and all vascular plant species were measured across up to seven fixed height tiers (Hurst et al., 2022). Within each tier, species were assigned a percentage or a cover class abundance value based on a modified Braun-Blanquet scale: <1%, 1%–5%, 6%–25%, 26%–50%, 51%–75%, and 76%–100%. To obtain a single species-level abundance value per plot accounting for overlap between tiers, we took the percentage or cover class midpoint for each plot/species/tier observation and combined the values following Fischer (2015). We combined species within the genera *Kunzea* and *Quintinia* to *K. ericoides* sensu lato and *Q. serrata* sensu lato, respectively, because the taxonomy supporting additional species in these genera is either disputed (Heenan et al., 2024) or not universally accepted (Dawson & Lucas, 2011). When species within these genera co-occurred, we combined abundance values following Fischer (2015).

We calculated mean species-level abundances for each LENZ Level II environment using the plot data, before relativizing to 100% cover. For LENZ Level II environments without plots ($n = 37$, covering 0.6% of the woody LCDB classes) we allocated mean species-level abundances from LENZ Level I environments. We assigned all species to one of three groups based on their likely supply level of floral resources to honeybees: (1) "high supply," species with copious nectar production known to be highly preferred by honeybees, taken from the New Zealand Trees for Bees flowering list (Trees for Bees, 2014); (2) "medium supply," other biotically pollinated species (McGlone & Richardson, 2023), including many species with small, inconspicuous flowers; and (3) "no/very limited supply," all abiotically pollinated species that lack nectaries. In the absence of detailed, species-specific floral resource supply data for New Zealand species, we allocated nectar and pollen production values species as follows: 602.6 and 250 kg ha^{-1} $year^{-1}$, respectively, for "high supply"; 301.3 and 125 kg ha^{-1} $year^{-1}$, respectively, for "medium supply"; and no nectar and pollen resources for "no/very limited supply." We calculated the "high supply" nectar value as the 85th percentile nectar supply value from a list of 152 nectar-bearing species (provided in supplementary tab. 11 of Baude et al., 2016) and took the "high supply" pollen value from the maximum of the full canopy production range (20–250 kg ha^{-1} $year^{-1}$) provided in Ausseil et al. (2018). Values for "medium supply" were half the "high supply" values. Although honeybees preferentially forage from flowers high in nectar (Nicolson, 2010; Seeley, 1986), we aimed to predict the total resource available at a particular location with values representing the amount of nectar and pollen available to honeybees from 1 ha of forest, assuming 100% cover. Since many of the native conifers are known to be good sources of spring pollen (Butz Huryn, 1995; Walsh, 1967), we applied "medium supply" pollen values (but "no/very limited supply" nectar values) for the following seven species: kauri (*Agathis australis*), kahikatea (*Dacrycarpus dacrydioides*), rimu (*Dacrydium cupressinum*), kawaka (*Libocedrus plumosa*), tōtara (*Podocarpus totara*), miro (*Pectinopitys ferruginea*), and mataī (*Prumnopitys taxifolia*) (see Walsh, 1967, pp. 6–7).

We calculated the proportion of flowering observations in each month for each species, for each genus, and overall across all species using phenology data mostly from Richardson et al. (2023). We extracted phenologies for the seven conifer species listed above from Walsh (1967). For each LENZ environment, we allocated nectar and pollen yields to each species based on their resource group (see above) scaled to their relative abundance and spread these values across the year based on their phenology. We used species-level phenologies (765/1271, or 60%, of biotically pollinated species; 96.8% of abundance-weighted records) when available; otherwise, we used genus-level (37%; 2.8% abundance-weighted) or overall mean (3%; 0.4% abundance-weighted) phenologies. We then calculated monthly sums across species to quantify LENZ-level nectar and pollen supply. We applied these to the areas of each LENZ environment within the native woody LCDB classes and assigned values for remaining areas based on their LCDB class (see above) then applied to a raster grid at a 100-m resolution matching the LENZ grids (Leathwick et al., 2002).

Honeydew produced by scale insects in some of the beech (*Fuscospora* spp.) forests of the northern South Island (Moller & Tilley, 1989) is another important source of sugars. These scale insects siphon sap from beech tree phloem, most of which is then excreted as a droplet on the end of an anal tube extending from the tree (Crozier, 1981). Honeydew is produced year-round, but particularly in spring (August–November) and autumn (March–April), in vast quantities of up to 4500 kg ha^{-1} $year^{-1}$ (Beggs et al., 2005). To incorporate this resource, we recreated the honeydew distribution from Beggs (2001) (Appendix S1: Section S4). We then applied our LENZ-level plant community predictions to the honeydew distribution to determine spatial abundance predictions of the four beech species known to have strong associations with honeydew-producing scale insects: red beech (*Fuscospora fusca*), black beech (*F. solandri*), mountain beech (*F. cliffortioides*), and hard beech (*F. truncata*) (Moller & Tilley, 1989). We took species-specific honeydew production values from tab. 6 of Beggs et al. (2005). For black beech, we calculated a mean from two years' presented data (2656 kg ha^{-1} $year^{-1}$). Production from red beech was measured across two tree size classes (small, large), also over two years, from which we took a mean (766.75 kg ha^{-1} $year^{-1}$). There are no equivalent measurements for mountain and hard beech, so we applied values from morphologically similar black and red beech, respectively, for these species, and an overall mean from the black and red beech values (1711.38 kg ha^{-1} $year^{-1}$) for hybrid beech records and genus-level identifications. We then scaled these values based on the predicted beech species' relative abundance and spread these across the year proportionally following the honeydew production phenology from Beggs et al. (2005; their tab. 3, 24-h closed quadrats). We applied these values based on the LENZ environments present in the 100-m resolution honeydew distribution (Appendix S1: Section S4), and summed these with the nectar grids (see above) to provide a measure of sugar production for all subsequent mapping and analyses.

Finally, because honeybees are unlikely to forage at temperatures below 10°C (Heinrich, 1979), we used monthly mean maximum temperature grids (Leathwick et al., 2002; McCarthy, Leathwick, et al., 2021) to remove available resources from areas ≤10°C (Appendix S1: Section S5). These analyses were completed in R 4.0.1 (R Core Team, 2021) using the "raster" (Hijmans, 2020), "rgdal" (Bivand et al., 2020), "fasterize" (Ross, 2020) and "sf" (Pebesma, 2018) packages.

Resource supply maps

To estimate the potential resource supply to an apiary located within a particular pixel, we followed the methods in Ausseil et al. (2018) to calculate the total resource within the bees' foraging range. While bees can travel up to 13 km from their hive in search of resources, 90% of foragers stay within 1 km (Garbuzov et al., 2015). The distance traveled by bees to collect resources depends on the availability and quality of resources nearby, the energy cost of collection, and the time of the year (Beekman & Ratnieks, 2000; Couvillon et al., 2015). Foragers can gain energy by consuming nectar, but not pollen, possibly explaining why nectar foragers fly further than pollen foragers (Couvillon et al., 2015). Foraging ranges were adjusted depending on the month of the year with greater foraging ranges in summer when the bees are more active (Couvillon et al., 2015). We applied conservative values ranging from 1 to 2 km in summer (December–February) and 0.5 to 0.25 km in winter (June–August) for nectar and honeydew, and pollen foragers, respectively (Appendix S1: Section S6), as per empirical (Couvillon et al., 2015; Seeley, 1995) and modeling (Ausseil et al., 2018) studies.

We calculated resource supply using circular convolution to produce a summation of nectar and pollen production over the foraging area (Appendix S1: Section S6). For nectar and honeydew, to reflect the energy needed to bring nectar back to the hive, we weighted this summation by a foraging efficiency function with an efficiency of one at a distance of zero, decreasing linearly to an efficiency of zero at the maximum foraging range. Monthly national supply maps (in kilograms per hectare per month) were produced using Python 3.7.10 (https://www.python.org/) using the "gdal" (GDAL/OGR contributors, 2021), "SciPy" (Virtanen et al., 2020) and "NumPy" (Harris et al., 2020) packages.

Land type analysis

We estimated the total amount of sugars (nectar and honeydew) and pollen within a range of designations commonly used to group land types in New Zealand to compare which land types have greater proportional areas of high resource production for honeybees (see Appendix S1: Section S7):

1. Native versus non-native/other landcover: almost half (49.5%) of New Zealand consists of indigenous landcover types (following Cieraad et al., 2015), dominated by Indigenous Forest (47.4%) and Tall Tussock Grassland (17.6%).
2. Public conservation land versus other: 33% of New Zealand is public conservation land administered by the New Zealand Department of Conservation and includes national parks, wildlife areas, reserves, and conservation areas. Terrestrial public conservation land is dominated by Indigenous Forest (54.2% of public conservation land), with substantial coverage of other indigenous classes like Tall Tussock Grassland (15.3%).
3. Māori land versus other: Māori land often has moderate amounts of woody vegetation cover (Harmsworth & Roskruge, 2014), including 27.2% cover of the Indigenous Forest LCDB class.
4. Pastoral farming (sheep and beef farming, and dairy farming): sheep and beef farming is the dominant land use type in New Zealand and covers more land area than all public conservation lands (Pannell et al., 2021). Sheep and beef farms contain more indigenous land cover than the intensively managed dairy farms (Foote et al., 2015; Norton et al., 2020; Pannell et al., 2021). Sheep and beef farms cover 37.0% of our study area and are dominated by High Producing Exotic Grassland (49.8%) but also have a substantial proportion of indigenous land cover (Indigenous Forest, 5.9%; Mānuka and/or Kānuka, 8.8%; Tall Tussock Grassland, 9.9%). Dairy farms cover 9.3% of our study area and are dominated by High Producing Exotic Grassland (85.0%) with a small proportion of Indigenous Forest (2.7%).

We made comparisons by allocating sugar and pollen production values to land types using a range of spatial datasets (Appendix S1: Section S7).

Historic vegetation cover analysis

To assess the impact of forest clearing following European colonization of New Zealand, and to quantify the possible benefit to honeybees from restoration, we predicted the provision of floral resources across the landscape as of c. 1840. We generated a map describing pre-European landcover by combining areas designated as tussock grassland in 1840, and historic (prehuman) indigenous forest from Ausseil et al. (2011). Since cleared areas in the North Island often reverted to woody seral ecosystems rather than grasslands between Māori (c. 1280; Wilmshurst et al., 2008) and European (c. 1840) arrival (Ausseil et al., 2011), we further categorized areas mapped as indigenous forest from Ausseil et al. (2011) and "Grassland and Scrub" from Weeks et al. (2013; their fig. 2, c. 1840) as "North Island Scrub." In these areas, we applied floral resource production values and phenologies from a mean of the seral LCDB categories (Broadleaved Indigenous Hardwoods, Mānuka and/or Kānuka, Fernland, Flaxland, Matagouri or Grey Scrub; Appendix S1: Sections S1 and S2). In areas of Indigenous Forest we applied floral resource production values based on LENZ Level II environments, as above. For remaining landcover types, we applied values based on LCDB. We removed pixels with monthly maximum temperatures of ≤10°C to account for honeybee foraging behavior. We also calculated differences in the provision of floral resource between past and current landcovers across New Zealand.

RESULTS

Floral resource production and supply

Floral resource production was greater in the summer months (Figure 1) when high-producing species were flowering (Figure 2) and warm temperatures facilitate foraging (Appendix S1: Section S5). Vegetated areas across most of the country are producing resources from November to March, but production and foraging activity is largely restricted to coastal regions north of the central South Island in the colder months (May–August; Figure 1). Annual production values of sugars (nectar and honeydew) range from 0 to 1417 kg ha^{-1} year^{-1} (Figure 1a) with low yields in non-vegetated areas (Appendix S1: Section S1) and high yields in honeydew-producing areas. Annual provision of nectar, excluding honeydew, in native woody landcover types range from 41.1 to 457.6 kg ha^{-1} year^{-1}. Pollen production generally follows that of nectar and ranges from 0 to 154.5 kg ha^{-1} year^{-1} (Figure 1b). High production occurs in native remnant vegetation, across the axial ranges of the North Island and the west coast of the South Island. Patterns of floral resource supply closely match that of production (Appendix S1: Section S6).

Pterophylla racemosa, a widespread and abundant tree, produces the most nectar of any plant species

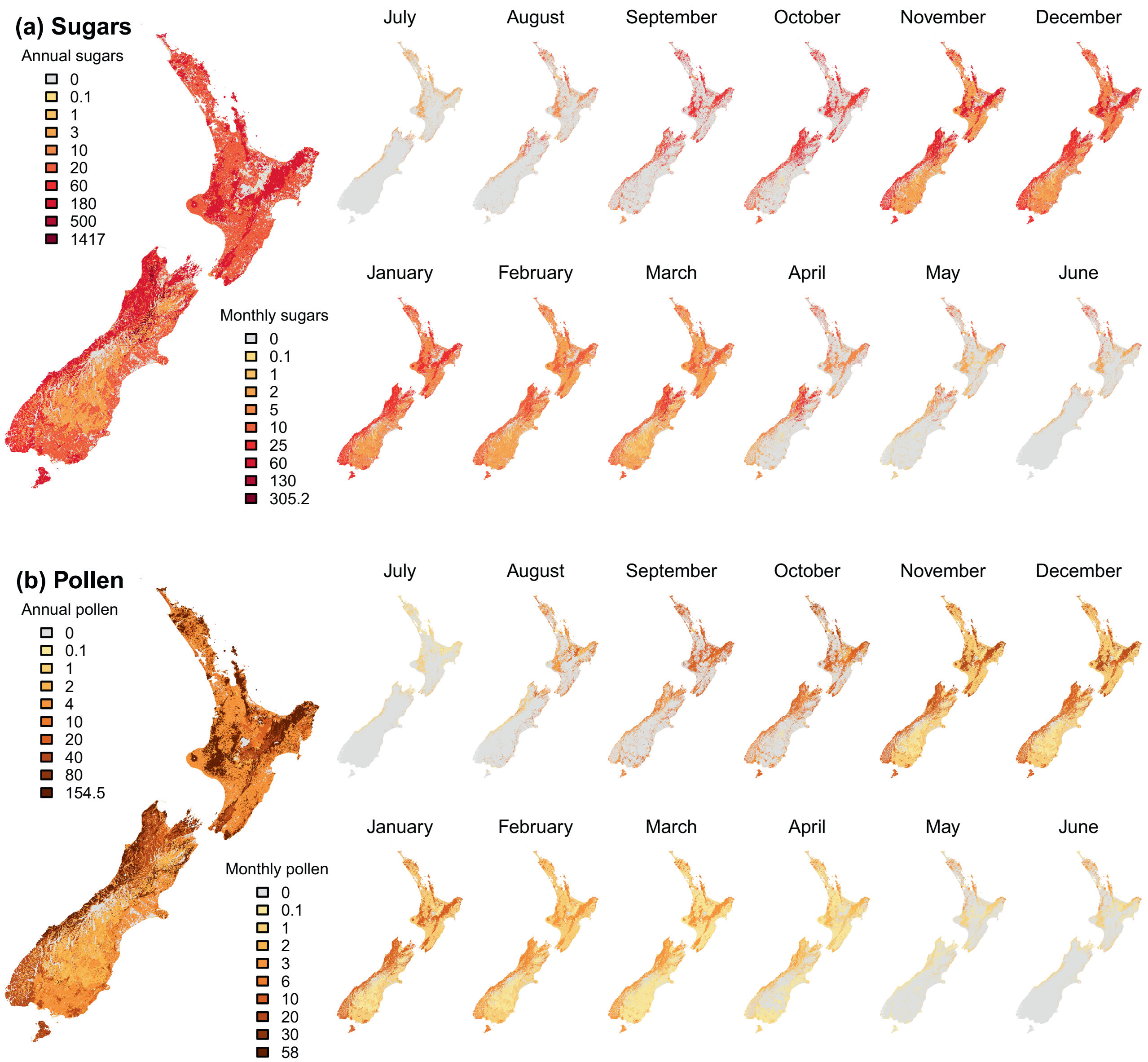

FIGURE 1 Predicted annual and monthly patterns of resource production for honeybees in New Zealand: (a) sugars (nectar and honeydew; in kilograms per hectare); (b) pollen (in kilograms per hectare).

in New Zealand, followed by *Beilschmiedia tawa* and *Pseudowintera colorata* (Figure 2). These three species flower primarily in the summer months. *Myrsine divaricata* is the highest ranked winter-flowering species. The Cunoniaceae, which includes *Pterophylla*, is the most productive plant family for resources (nectar and pollen production), closely followed by the Myrtaceae (Figure 3) which has 6 species in the top 25 most productive plant species (Figure 2).

Indigenous vegetation contribution to floral resources and land type comparisons

Widespread forest clearing in the North Island following European colonization of New Zealand has resulted in substantial decreases in floral resource production (Figure 4). Deforestation has also contributed to losses in floral production in coastal areas of the South Island. Increases in floral production are restricted to reforested areas in the central North Island and northeastern South Island. Zero or little change occurred in areas with unaltered land cover, or where conversions have been less severe, such as shifts from Tall Tussock Grassland to High Producing Exotic Grassland (both have similar floral resource production values; Appendix S1: Section S1). This shift is widespread in the South Island, where native grasslands have been converted to higher production systems supporting livestock grazing (Figure 4). We estimate the total national annual production of sugars has dropped from 4.19 to 2.57×10^{-9} kg (38.8% loss) and pollen

Species	Family	Total nectar (kg year^{-1}) × 10^{-7}	Total pollen (kg year^{-1}) × 10^{-7}	Phenology
Pterophylla racemosa	Cunoniaceae	27.05	11.22	
Beilschmiedia tawa	Lauraceae	11.36	4.71	
Pseudowintera colorata	Winteraceae	10.05	4.17	
Griselinia littoralis	Griseliniaceae	9.65	4.00	
Melicytus ramiflorus	Violaceae	7.83	3.25	
Quintinia serrata	Paracryphiaceae	7.76	3.22	
Metrosideros umbellata	Myrtaceae	7.03	2.92	
Carpodetus serratus	Rousseaceae	5.23	2.17	
Ripogonum scandens	Ripogonaceae	4.44	1.84	
Hedycarya arborea	Monimiaceae	4.42	1.83	
Metrosideros diffusa	Myrtaceae	4.17	1.73	
Knightia excelsa	Proteaceae	4.02	1.67	
Freycinetia banksii	Pandanaceae	3.88	1.61	
Pseudopanax crassifolius	Araliaceae	3.42	1.42	
Myrsine divaricata	Primulaceae	3.40	1.41	
Neomyrtus pedunculata	Myrtaceae	3.08	1.28	
Leucopogon fasciculatus	Ericaceae	2.79	1.16	
Rhopalostylis sapida	Palmae	2.79	1.16	
Leptospermum scoparium	Myrtaceae	2.69	1.12	
Rubus cissoides	Rosaceae	2.45	1.02	
Kunzea ericoides	Myrtaceae	2.37	0.98	
Dysoxylum spectabile	Meliaceae	2.24	0.93	
Metrosideros fulgens	Myrtaceae	2.23	0.92	
Elaeocarpus dentatus	Elaeocarpaceae	2.18	0.91	
Schefflera digitata	Araliaceae	1.89	0.79	

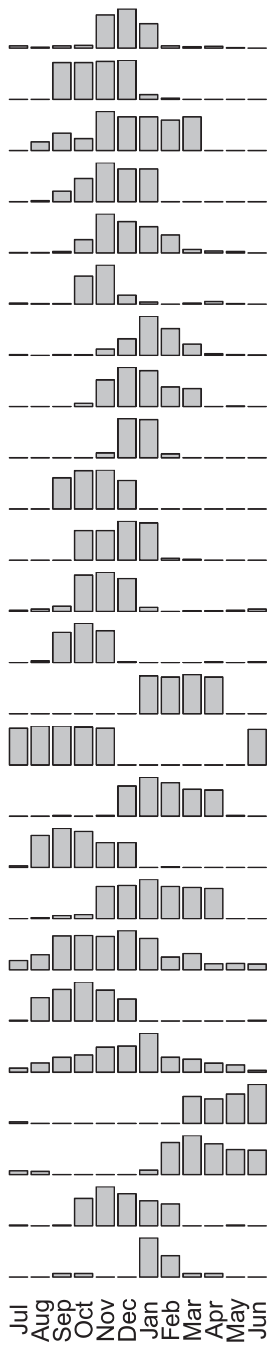

FIGURE 2 Top 25 plant species ranked based on their annual floral nectar (excluding honeydew) and pollen supply across New Zealand's mapped natural forests and shrublands.

production has dropped from 1.33 to 0.87 × 10^{-9} kg (34.7%) due to forest clearance since European colonization. Indigenous landcover now covers 49.5% of New Zealand, but still produces most of the country's floral resources (Figure 5).

Despite covering 33% of New Zealand (Appendix S1: Section S7), public conservation lands contribute over half of the floral resource production and have more high-producing areas than non-public conservation land (Figure 5). Māori land (5% of New Zealand) contributes only a small total proportion of nationwide floral resource, but more per hectare than non-Māori land, and has a greater proportion of areas of high floral production. Sheep and beef farms have a slightly greater proportion of high-producing areas than dairy farms.

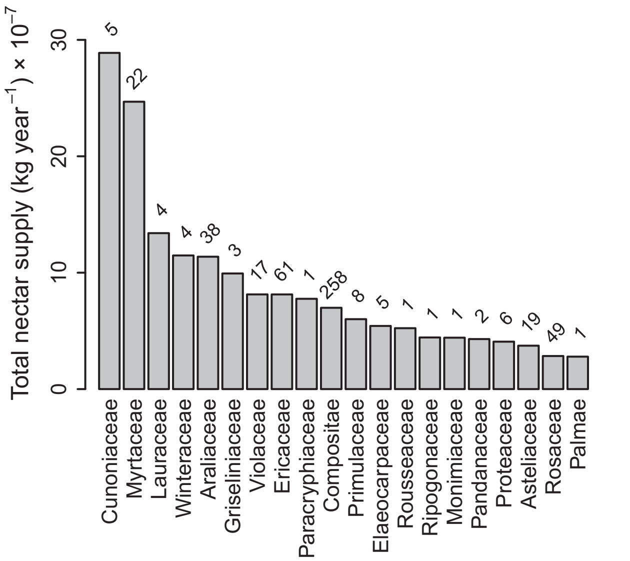

FIGURE 3 Ranking of the top 20 plant families based on their mean annual floral nectar production across New Zealand natural forests and shrublands. Numbers above bars indicate the number of species identified in forest and shrubland vegetation survey plots within each family which may include native and non-native species.

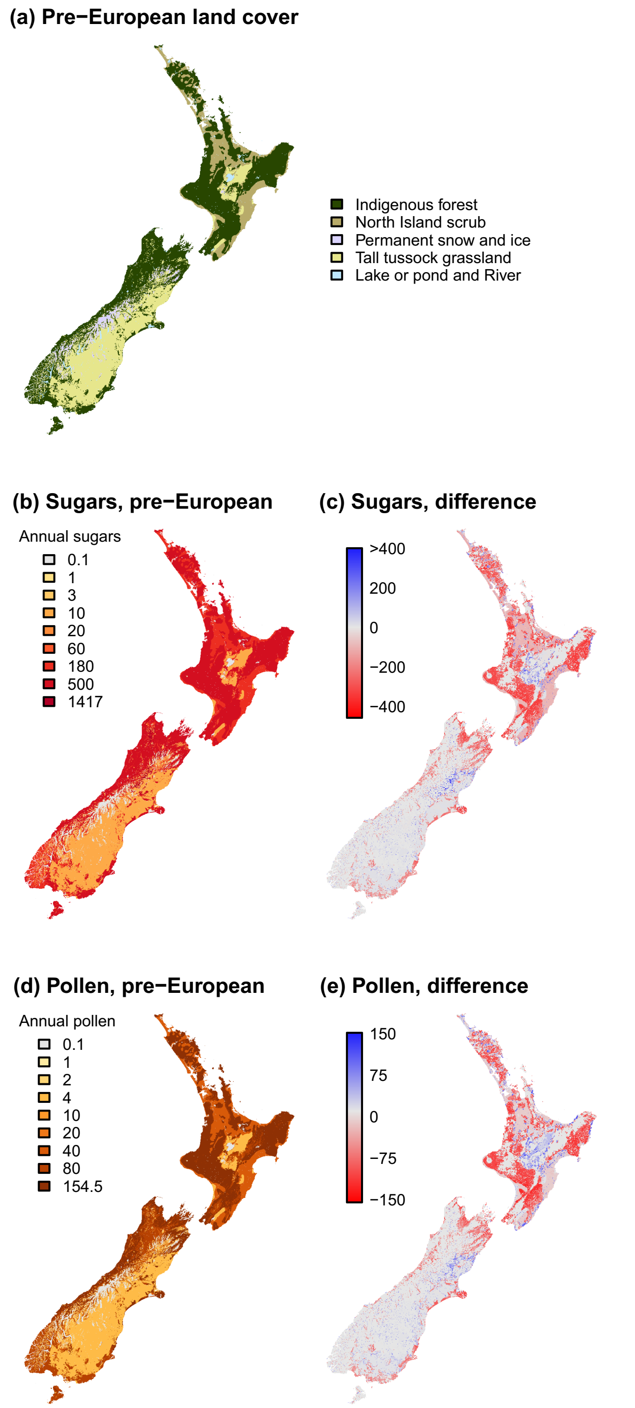

FIGURE 4 Mapping land cover, floral resources (in kilograms per hectare), and predictions of resource change (in kilograms per hectare), in New Zealand through time: (a) land cover types before widespread European settlement in c. 1840; (b) pre-European sugar production; (c) predicted difference for present-day sugar production; (d) pre-European pollen production; (e) predicted difference for present-day pollen production.

DISCUSSION

Determining the rates of floral resource production over large spatial scales is an important step for quantifying their ecosystem-level contribution as food for pollinators and the benefits of ecosystem conservation and restoration. It also supports integrated scenario analysis on nature's contributions to adaptation (Richards et al., 2023), clarifies the impacts of clearing vegetation, and supports the management of commercial honeybee enterprises. Here, we present a method to estimate floral production at a nationwide scale across a complicated landscape consisting of a range of intensities of agricultural and production lands, urban areas, and native and regenerating forests, grasslands, and alpine areas. Forests that produce honeydew, restricted to beech (Nothofagaceae) forests in the northern South Island, are easily the most productive areas nationally in terms of sugars. Pollen production is highest in indigenous forests along the axial ranges of the North Island and the west coast of the South Island. Production of floral resources is highly seasonal with low production during the winter months (May–July) when only a small number of species flower. Our maps highlight the spatial and temporal variability in resource supply, and also potential opportunities for placement of honeybee hives during the winter months.

Beekeepers find it difficult to manage the gap in pollen supply in spring (c. October) as most plant species of non-native landcover types have yet to flower (Appendix S1: Section S2; Ausseil et al., 2018). Spring pollen is essential for honeybees as the brood is increasing in numbers in preparation for summer (Mattila & Otis, 2006).

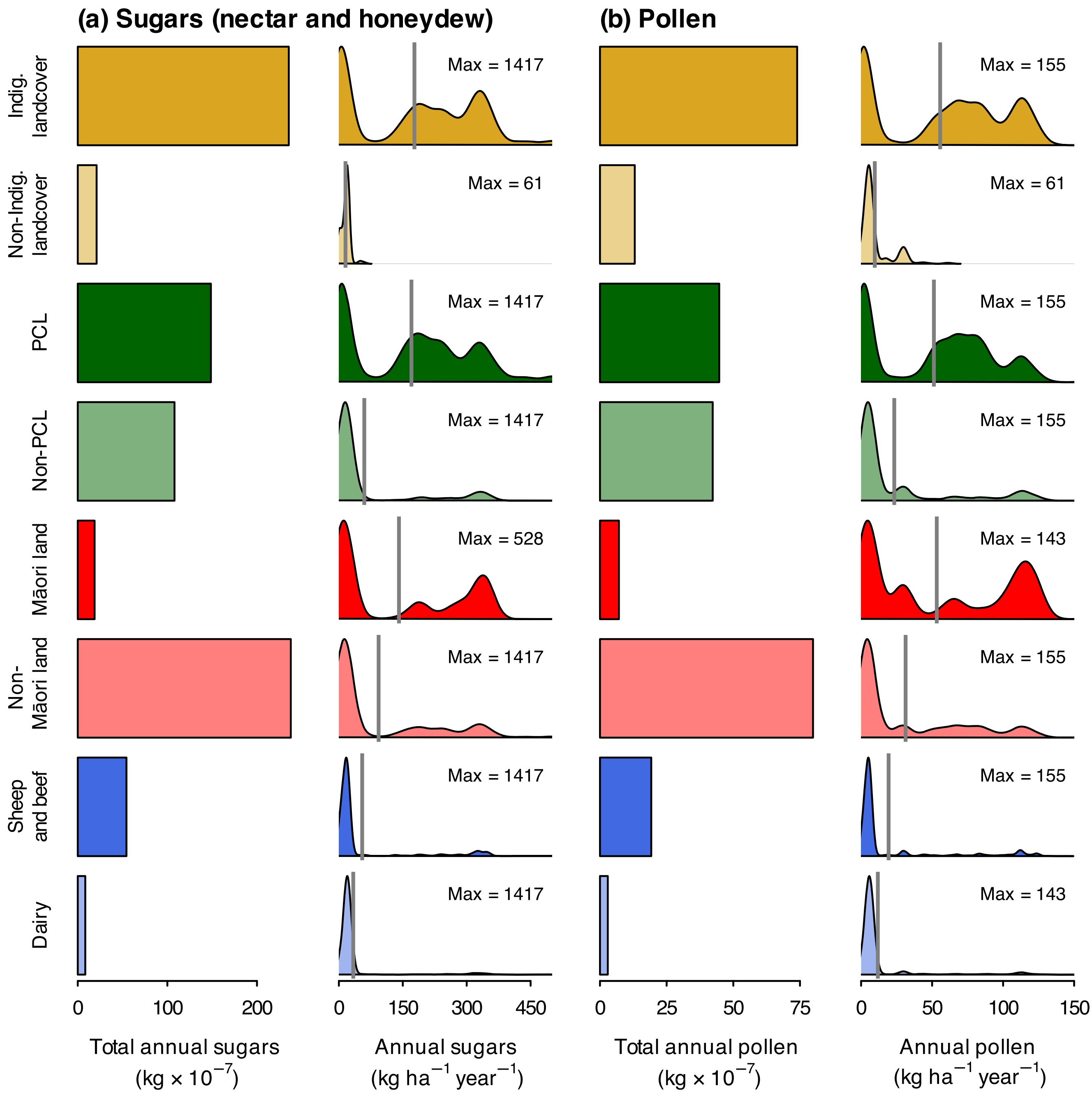

FIGURE 5 Total production and distribution of production values of floral resource for honeybees produced by a range of land types commonly used to group land in New Zealand: (a) sugars (nectar and honeydew); (b) pollen. Distributions were produced using values extracted from 10,000 random locations. Vertical gray bars indicate the mean annual production for each land type and resource. PCL, public conservation land.

This is particularly problematic in areas with a dense concentration of hives, usually close to species producing high-value honey such as mānuka (Brown et al., 2018). Supplements are usually provided, but fresh pollen from a diverse range of plant species promotes honeybee health (DeGrandi-Hoffman et al., 2016). During early spring (September–October), abundant nectar and pollen are produced across much of the native forest vegetation, which might provide an opportunity for overwintering hives.

There are no social bee species native to New Zealand, with pollination provided historically by solitary bees, other insects, birds, bats, and reptiles (Newstrom & Robertson, 2005). Some evidence suggests that competition between managed honeybee hives and native pollinators is limited (Butz Huryn, 1997; Donovan, 1980), but further research is needed to understand the impact of honeybee competition on native pollinating fauna (Beard, 2015; Howlett & Donovan, 2010; Iwasaki et al., 2015). Honeybees can deter other bee species from high-quality forage (Gross, 2001; Roubik, 1978), possibly displacing natives (Ginsberg, 1983; Schaffer et al., 1983), and evidence-based management of hive placement and density is required to balance hive productivity with ecosystem services and biodiversity values. This could be supported by our maps which provide an estimate of the floral production at a given location and month to ensure that: (1) areas are not overstocked above the carrying capacity of the vegetation; and preferably (2) that hive numbers are restricted to a only a proportion of the total theoretical production of an area, leaving the remainder for native pollinators.

Apiary site overcrowding (Brown et al., 2018) is particularly problematic in places easily accessible and close to vegetation producing high-value honey (e.g., mānuka). Overcrowding can result from an overestimate of the carrying capacity of a property, and is exacerbated by "boundary stacking" (McPherson, 2016) where hives are placed just outside properties with high-value species. The Department of Conservation manages hive concessions on public conservation lands, but little research informs this process (Beard, 2015). As hive numbers have been increasing in New Zealand (Ministry for Primary Industries, 2020), high-resolution data (both spatial and temporal) will be required to limit overcrowding and guide decisions, and to reduce competition with native pollinators. The maps presented here could provide the basis for a concession process that incorporates both location and season based on the productivity of the surrounding landscape. More research is needed on the foraging efficiency of honeybees and the requirements of native pollinators, but in the short term, a conservative threshold could be applied (e.g., that hive requirements do not exceed a nominal percentage of the predicted production within their range).

In natural forests and shrublands, nectar supply is overwhelmingly produced by two plant families: Cunoniaceae and Myrtaceae. Within the Cunoniaceae, almost all supply is produced by kāmahi (*Pterophylla racemosa*), a widespread and abundant species (Wardle & MacRae, 1966), yielding a popular monofloral honey. The Myrtaceae, an ecologically and functionally important family in New Zealand (Jo et al., 2022; McCarthy et al., 2024), ranks next, with six of the top 25 ranked species. The most productive species of Myrtaceae is southern rātā (*Metrosideros umbellata*) which produces a popular honey and is widespread and abundant in native forest in cooler, montane forests (McCarthy, Wiser, et al., 2021; Wardle, 1971).

We showed that land type substantially affects nectar and pollen supply. Māori-owned land covers 1.33 million ha (5.0%) of New Zealand, mainly adjoining public conservation land and retired/marginal agricultural land (Harmsworth & Roskruge, 2014). These less intensively managed areas commonly comprise regenerating forests and shrublands, often dominated by mānuka, with honey generating significant income for Māori (Harcourt et al., 2022). This successional vegetation covers 12.3% of Māori-owned land (Mānuka and/or Kānuka; Appendix S1: Section S7) which, along with a high proportion of native forest (Indigenous Forest; 27.2%), means that Māori land, while producing a minor part of the total national nectar production, is more productive than non-Māori land. Both public conservation land and areas with indigenous landcover produce far greater amounts of floral resources than non-public conservation land and non-indigenous landcover.

Neither sheep and beef farms nor dairy farms produce large quantities of floral resources, despite covering almost half of the country (12.4 million ha; 46.3%). Sheep and beef farms produce more floral resources than dairy farms per hectare, primarily because they are farmed less intensively and have retained a greater proportion of woody vegetation cover (Fernandez, 2017). Various policies have promoted the retention or regeneration of woody vegetation, which is more easily achieved on less intensive farming systems (Pannell et al., 2021). Both in New Zealand (Norton et al., 2020) and internationally (Tilman et al., 2001), agricultural activities are under substantial pressure to reduce and reverse the environmental impact of land use change and habitat degradation (Newbold et al., 2015). While restoration of native habitat is beneficial for conservation, landscape connectivity, carbon sequestration, and a range of ecosystem services like erosion prevention, we show that restoring indigenous land cover types would also be beneficial for pollinators.

Almost half of New Zealand is covered by indigenous land cover types, but this area produces 92% and 85% of the country's nectar and honeydew, and pollen, respectively. The combined effect of Māori- and European-era clearances has left <30% of the prehuman forest cover (Ewers et al., 2006). Drier coastal areas were burnt extensively by Māori, with European-era clearing focused on wetter areas of the North Island and the northern and eastern extents of the South Island (Leathwick, 2001; McGlone, 1989; Newsome, 1987). Most of these forests were cleared in the early period of European arrival, primarily by fire (Perry et al., 2014), as early settlers were encouraged to farm and to clear land for agriculture, even in remote areas (Wynn, 2002). Timber harvesting led to further clearance, especially in the late nineteenth century (McGlone et al., 2022). Land cover changes associated with European settlement have resulted in a dramatic decrease in floral resource production of 38.8% and 34.7% for nectar and pollen, respectively. These decreases have been mainly in the wetter and warmer forests of the North Island, which were still forested at the time of European colonization.

While we endeavored to keep our estimates as accurate as possible, the uncertainty of floral resource production is still great. Inaccuracies in maps used to depict environment and land cover will add to this uncertainty. As will our species compositions derived from environment classes and vegetation plots, and our temperature-based mask, which will become increasingly less accurate under climate change. Advancements in community-level modeling approaches (e.g., Mokany et al., 2011) and remote sensing of floral resources (Gonzales et al., 2022) could be valuable avenues for future refinements. Finally, a lack of available production data (i.e., from honey bee hive yields, which are commercially sensitive and biased toward productive areas) meant we were unable to formally validate our maps. As such, our maps are most valuable as a comparison between environments and locations—perhaps aiding in guiding restoration and enhancement of vegetation—and comparative scenario analyses rather than for direct calculation of potential production (or honey yield) for a particular location. Future refinements could incorporate within-species variability in phenology, which can be substantial, especially for widespread species. Maps could also be validated through a comparison with actual hive production data, though this would require the release of commercially sensitive data and would ideally include data from areas with low production (where hives are rarely located). Species-level forage preferences for honeybees could be specifically accounted for to assist with management of hives.

CONCLUSIONS

The spatial data produced here provide an estimate of production and supply of floral resources across New Zealand. Our quantitative approach uses substantial data from vegetation plots, as well as spatial layers describing land cover and environment. These have been produced at monthly intervals and incorporate species-level flowering phenologies. We detail a method that can be applied elsewhere. Within New Zealand, these maps provide an understanding of how the national floral production is distributed across space and time, providing a useful tool for the management of complex ecological systems. The maps can be used to help management of honeybee hive placement and stocking density, contributing to a more sustainable industry that minimizes competition with native pollinators. They can also be used to assess the benefits and consequences of land use change and ecological restoration, while also helping inform decision-making on resource use limits.

AUTHOR CONTRIBUTIONS

James K. McCarthy, Sarah J. Richardson, Gary J. Houliston, and Anne-Gaelle E. Ausseil conceived the ideas and designed the study. James K. McCarthy, Sarah J. Richardson, Matt S. McGlone, and Anne-Gaelle E. Ausseil generated and collated the data. James K. McCarthy and Thomas R. Etherington conducted the analysis. James K. McCarthy led the writing. All authors contributed to the drafts and gave final approval for publication.

ACKNOWLEDGMENTS

Plot data were drawn from the National Vegetation Survey Databank (http://nvs.landcareresearch.co.nz); we thank Ella Hayman, Elise Arnst, and Susan Wiser for facilitating access. These data included plots surveyed between January 2002 and March 2007 by the LUCAS programme for the Ministry for the Environment and data from the Department of Conservation which is licensed for re-use under a Creative Commons Attribution 4.0 International License. We thank the Honey Landscape project steering group for advice, and Garth Harmsworth for help describing Māori land. Helen O'Leary and a reviewer provided helpful comments on the manuscript. This project was funded by the Ministry for Business, Innovation and Employment through their Endeavour (Programme C09X1608) and Strategic Science Investment funds. Open access publishing facilitated by Landcare Research New Zealand, as part of the Wiley - Landcare Research New Zealand agreement via the Council of Australian University Librarians.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (McCarthy et al., 2025) are available from the Manaaki Whenua – Landcare Research DataStore at https://doi.org/10.7931/ervd-xs26, including plant community predictions per LENZ Level II environment, all national-scale predictions of nectar, pollen, and honeydew (pre-European, contemporary production, and contemporary supply), and the pre-European landcover map for New Zealand, along with data informing species-level pollination mode and flowering phenology. Vegetation plot data are archived in the New Zealand National Vegetation Survey Databank (https://nvs.landcareresearch.co.nz) and can be requested using the plot IDs provided in the Manaaki Whenua – Landcare Research DataStore release.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: McCarthy, James K., Sarah J. Richardson, Gary J. Houliston, Thomas R. Etherington, Matt S. McGlone, and Anne-Gaelle E. Ausseil. 2025. "National-Scale Mapping of Potential Floral Resources for Honeybees and Native Pollinators in New Zealand." *Ecological Applications* 35(3): e70041. https://doi.org/10.1002/eap.70041