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Assessing unintended human-mediated dispersal using visitation networks

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Abstract

1. Human visitors are associated with the unintended dispersal of weeds, seeds and pathogens across ecological communities. With the increasing popularity of nature-based tourism, access to protected areas has increased, in turn increasing the risks of unintended dispersal of exotic species to these areas.
2. Here, we assess the potential contribution of both international and domestic visitors travelling within New Zealand to the spread of exotic species. To get an overview of the visitors' travelling patterns across the country, we constructed visitation networks at two spatial scales—a regional scale (which is a coarse scale) and a local territorial scale (which is a finer scale).
3. We then used a Mixed Membership Stochastic Block Model to identify characteristic groups of visitors and places based on the similarities of the visitors' travelling patterns across the country. Overall, we found that there are 10 characteristic groups of visitors travelling to 12 characteristic groups of places at the regional scale and 6 characteristic groups of visitors travelling to 6 characteristic groups of places at the territorial scale.
4. The resulting characteristic travelling patterns of the visitors across New Zealand further allowed us to estimate the different visitor groups' likelihood to travel to protected areas. Overall, we found that some visitor groups are much more likely than others to travel to protected areas of high protection status, at both spatial scales.
5. *Synthesis and applications*. Our results highlight the importance of accounting for human behaviour—that is, understanding how visitors travel to places—when assessing human-mediated dispersal. More specifically, we illustrate how to assess the relative contribution of a potential vector dispersing exotic species based on their travelling patterns—especially in cases where the target exotic species are not yet identified or when there is limited information regarding the dispersal routes of exotic species and their potential vectors. As a result, our work offers a holistic perspective on human-mediated dispersal of exotic species. Moreover, it provides a potential baseline against which both field biologists and practitioners can identify areas that would benefit from further investigation to better understand invasion processes in their focal systems.

KEYWORDS
biological invasion, ecological management, human behaviour, invasion risk, Mixed Membership Stochastic Block Model, risk assessment, travelling pattern, visitation networks

1 | INTRODUCTION

Human-mediated dispersal is considered a major contributor to biological invasion (Clifford, 1959; Hulme, 2009; Mack et al., 2000; Seebens et al., 2013). As a consequence of globalisation, transportation networks are being extensively developed, and this development results in the spread of exotic species over larger and longer distances (Hulme, 2009; Seebens et al., 2013, 2017). To date, over thirteen thousand exotic plant species have been recognised as naturalised worldwide as a result of human-mediated dispersal (Van Kleunen et al., 2015). Similar patterns are also observed at finer scales; for example, various studies have identified high abundances of exotic species within protected areas (Clifford, 1959; Foxcroft et al., 2011; McNeill et al., 2011; Pickering & Mount, 2010; Pickering et al., 2011). To reduce the risks of invasion, managers use various tools, often including early detection, monitoring and eradication programs (DiTomaso, 2000; Hulme et al., 2014; Ruiz & Carlton, 2003). Despite these precautionary measures, however, some exotic species still manage to escape in the wild (Hulme, 2009; Reichard, 2001). Though not all the introduced species become invasive, identifying paths and areas where they are more likely to spread is crucial, as it might help managers to prioritise sites for management and monitoring purposes (Hulme, 2009; Pickering & Mount, 2010). In the case of unintended human-mediated dispersal, this can be particularly challenging; unless an exotic species undergoes exponential population growth in the newly introduced area, its presence and spread can often go undetected (Essl et al., 2015a). As a result, potential paths along which exotic species are suspected to be introduced or spread are generally only identified a posteriori—often in response to high abundance of the exotic species (Essl et al., 2015b). Consequently, the cost associated with the management and eradication of these exotic species is often high.

Reducing the management cost of unintended human-mediated dispersal ideally entails prioritising the detection of potential dispersal routes and quantifying how humans contribute to biological invasion (Essl et al., 2015a; Hulme, 2009; Pyšek et al., 2011). Although empirical studies have identified visitors as dispersers of exotic species to protected areas over both short and long distances (Clifford, 1959; McNeill et al., 2011; Pickering et al., 2011), very little is known about the visitors' role in contributing to biological invasion. Moreover, such studies are often limited or restricted to certain dispersal routes thereby making it difficult to get a broad overview of the extent to which visitors might be dispersing exotic species. Here, we propose using the travelling patterns of visitors as a proxy of propagule pressure—that is, the number of exotic species visitors could introduce—to assess the visitors' risks of dispersal while travelling within a country.

In our current study, we focus on assessing visitors' travelling patterns within New Zealand. Specifically, we analysed visitation data from both international and domestic travellers at two different spatial scales—a regional scale (which is a coarse scale) and a territorial scale (which is a finer scale). Regardless of the spatial scales at which these data were analysed, we found that individuals tend to share similarities in their travelling patterns. This allowed us to categorise the visitors' travelling patterns into different 'typical' patterns, each of which describes characteristic way visitors tend to travel within and across New Zealand. We further showed how such travelling patterns can be used to estimate visitors' likelihood of travelling to protected areas. In doing so, our study highlights the importance of incorporating and understanding human behaviour when assessing human-mediated dispersal—especially when either the identity of the target exotic species and/or the dispersal routes are unknown.

2 | MATERIALS AND METHODS

In order to assess the risk of visitor-mediated dispersal within New Zealand, we focused on characterising and understanding how visitors travel across the country. We specifically used a network model that allows us to group the visitation data based *only* on visitor travelling patterns. In the following sections, we describe: (a) the visitation data, (b) the network model used to understand the visitors' travelling patterns and (c) how we estimated the likelihood of visitor-mediated dispersal to protected areas across New Zealand.

2.1 | Visitation data in New Zealand

To analyse the visitors' travelling patterns across New Zealand, we extracted data from three national surveys: the International Visitor Survey (Ministry of Business Innovation & Employment, 2016b), the Domestic Travel Survey (Ministry of Business Innovation & Employment, 2016a) and the National Survey of New Zealanders (Department of Conservation, 2016). Note that all three surveys target, for each Regional Council, a quota of visitors from different nationalities and ethnicities in order to ensure that the collected data are representative of all visitors travelling across New Zealand (Ministry of Business Innovation & Employment, 2016a, 2016b; Department of Conservation, 2016). Since each survey was initially designed for a slightly different purpose, we observed a mismatch in their spatial resolution. We therefore used the Regional Councils (coarse spatial scale) and Territorial Authorities (fine spatial scale)—which are official jurisdiction boundaries across New Zealand—to standardise the

visitation dataset (Table S1). To do this, we used the R packages RGDAL (Bivand et al., 2015) and RGEOS (Bivand et al., 2017) to map the different places from the visitation data onto New Zealand's 17 Regional Councils and 68 Local Territorial Authorities boundaries. Note that these two different spatial scales provide us with two biologically useful perspectives: environmental monitoring and eradication programs of exotic species in New Zealand are carried out at the Regional Councils scale while land use and resource management are monitored at the Territorial Authorities scale (Department of Internal Affairs, 2017; Sullivan et al., 2005).

2.2 | Mixed Membership Stochastic Block Model

To understand the different visitor–place interactions within the data, we first represented the visitation data as a bipartite network—where the itinerary of any given visitor (i.e. their trip) can be decomposed into a series of visitor–place interactions (Figure 1). In this network, visitors and places are represented as sets of nodes, and the visitor–place interactions are represented as links connecting the nodes. To further understand these different visitor–places interactions within the bipartite network, we then examined the visitation data using Stochastic Block Models—a class of probabilistic generative network models that describes the general structure of large–scale networks (Airoldi et al., 2008, 2014; Erosheva et al., 2007; Holland et al., 1983; Wang & Wong, 1987). In these models, nodes that interact in a similar fashion are assumed to belong to characteristic groups and the probabilities of interaction between nodes can then be estimated based on their group memberships.

We specifically used the Mixed Membership Stochastic Block Model (MMSBM) inference approach of (Godoy-Lorite et al., 2016). Unlike the traditional Stochastic Block Models, the MMSBM allows the nodes to belong to a mixture of groups (Airoldi et al., 2008, 2014; Godoy-Lorite et al., 2016). In our case, this implies that, instead of assuming that all visitors with similar interests will belong to the exact same group and thus behave in an identical way, visitors are allowed to belong to a mixture of groups. This is important because it allows the model to account for the mixed behaviours of visitors. Similarly, places receiving visits from different visitor groups will also belong to a mixture of groups. Following this, the probability of interaction between a given visitor and a given place is then estimated as a function of the group memberships of both visitor and place.

Given a network of visitors and places, and assuming that there are K different groups of visitors and L different groups of places, the MMSBM estimates the following: the probability θ_{uk} describing the likelihood that every visitor u belongs to every group k (such that $\sum_k \theta_{uk} = 1$); the probability η_{il} describing the likelihood that every place i belongs to every group l (such that $\sum_l \eta_{il} = 1$); and the probability of an interaction between each visitor and place group p_{kl} (such that $0 \leq p_{kl} \leq 1$). A visitor group k can either tend to be connected to all place groups or not, such that $0 \leq \sum_l p_{kl} \leq l$. Across all visitor groups, this implies that things can vary between all visitor groups being

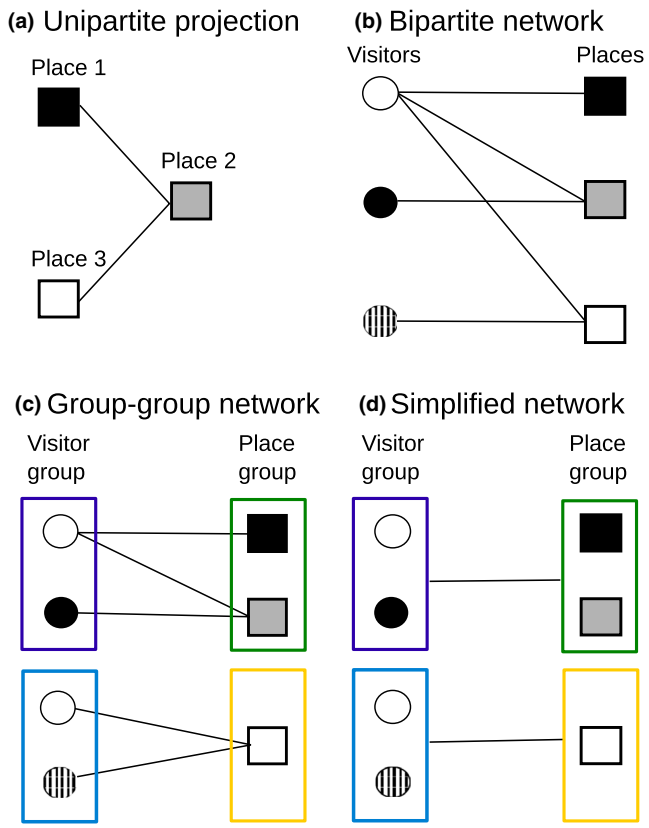

FIGURE 1 A network approach to represent visitation data. (a) A unipartite projection of the data would equate to a place–place network where nodes represent places and links represent trips travelled between places. (b) A bipartite network instead has two node types, where circles and squares represent visitors and places, respectively. The links connecting visitors and places represent trips of a given visitor to a given place. (c) Groups are identified based on the similarity of the visitor–place interactions within the bipartite network. (d) Block structure representation of the visitor–place network—giving an overview of the patterns of interactions between visitor groups to place groups identified. Note that in the case of the Mixed Membership Stochastic Block Model employed here, both visitors and places can belong to a mixture of groups

fully connected to all place groups or not at all ($0 \leq \sum_k \sum_l p_{kl} \leq kl$). Consequently, the probability of observing a visitor u travelling to a place i can be described by

$$p(u \rightarrow i) = \sum_{k,l} \theta_{uk} \eta_{il} p_{kl}. \quad (1)$$

Since one cannot know the optimal number of groups of either visitors or places prior to data inspection, we fit the MMSBM with different K–L combinations—that is, K varying between 1 to 12 and L varying from 1 to 12 at the regional scale, and K varying from 1 to 9 and L varying from 1 to 9 at the territorial scale. Based on the Bayesian information criterion (BIC) of these fits (Supporting Information), we then identified the optimal number of visitor and place groups at each spatial scale (Tables S4 and S5).

We performed 500 independent runs of the MMSBM with different initial conditions to create posterior distributions of the

most likely parameter values θ_{uk}, η_{il}, p_{kl} given the data (Godoy-Lorite et al., 2016). For every independent run, however, the MMSBM randomly assigns different group labels to the visitor and place groups (Supporting Information). Since here we are particularly interested in characterising the behaviour of different visitor groups, distinguishing whether a given visitor group is consistently observed to travel to the same subset of place groups across the 500 independent runs of the model is crucial. Hence, we had to ensure that the label assigned to a particular place or visitor group was consistent across all independent runs of the model (Figure S3). However, as we had no prior knowledge of 'true' labels of the visitor and place groups, we considered the solution having the greatest likelihood as our 'true' labels of the visitor groups and place groups. By using an optimisation algorithm, we then permuted the group labels across the visitor and place groups obtained from separate runs of the model to optimally match the labels across all independent runs. We then computed the average of the model parameters (Supporting Information).

2.3 | Identifying potential areas at risk of visitor-mediated dispersal

In the following sections, we show how one can assess the relative risks of visitors in dispersing exotic species to protected areas. More specifically, we demonstrate how we used the characterised travelling patterns of visitors generated from the MMSBM to estimate the visitors' likelihood to travel to protected areas within New Zealand. We then show how we can combine those findings and occurrence data of pest plants to identify potential areas at risk of future spread.

2.3.1 | Estimating the likelihood of travelling to protected areas

To assess the visitors' potential impacts in protected areas within New Zealand, we next estimated their likelihood to travel to these areas. As we were particularly interested in investigating whether different visitor groups are likely to have different impacts, we used the relative difference in the visitors' travelling patterns to estimate their likelihood to visit protected areas, where relative difference was given by rescaling the p_{kl} as *z*-scores. Specifically, the latter was calculated as $z_{kl} = \frac{p_{kl} - \overline{p_{.l}}}{\sigma_{p_{.l}}}$, where p_{kl} is the aforementioned probability of visit between visitor group *k* and place group *l*, $\overline{p_{.l}}$ is the mean probability of a visit to place group *l* calculated across all visitor groups, and $\sigma_{p_{.l}}$ is the standard deviation across all visitor groups.

Assessing the visitors' likelihood of travelling to protected areas is equivalent to estimating the probability of visitor groups interacting with place groups characterised as protected areas. However, due to the lack of visitation data that explicitly accounts for visitors travelling to specific protected areas within each region, we assumed that the likelihood of any particular visitor group to travel *to protected areas* in each region would be directly proportional to that region's percentage cover of protected area. Since this assumption may not be universally true, we will return to this in Section 4.

To identify the protected areas across the country, we used the Protected Area Network New Zealand defined by Manaaki Whenua–Landcare Research (Manaaki Whenua–Landcare Research, 2017; Rutledge et al., 2004). According to this classification, the protection status of a given protected area is defined as a value *j* ranging between 1 and 5, indicating low and high priority of biodiversity protection, respectively (Manaaki Whenua–Landcare Research, 2017; Rutledge et al., 2004). Following this definition, we estimated the average protection status for all place groups. To do so, we mapped the Protected Area Network onto the Regional Council and Territorial Authorities boundaries to calculate the relative percentage cover of protected areas within each jurisdiction. Hence, the proportion of any protected area of given status *j* in each given region (or territory) *i* is estimated as

$$a_{ij} = \frac{\text{Area (Protected area}_j \cap \text{Jurisdiction}_i)}{\text{Area (Jurisdiction}_i \cap \text{New Zealand)}}. \tag{2}$$

Using the group membership of the places (i.e. η_{il} estimated by the MMSBM), we then calculated the likelihood that each place group *l* consists of a given protection status *j* ($\sum_i \eta_{il} a_{ij}$). Following this, the likelihood for a given visitor group *k* to travel to place groups characterised by a protection status of level *j* can be described as

$$v^*_{kj} = \sum_l \left(p_{kl} \sum_i \eta_{il} a_{ij} \right). \tag{3}$$

2.3.2 | Assessing the relative risks of visitor groups

From a visitor-mediated dispersal point of view, we considered visitors as dispersers of exotic species and places as the potential impacted areas. To assess the relative risks of visitors in dispersing exotic species, we further used the protection status of protected areas as an indicator of the relative risks for a given visitor group to encounter exotic species. We again used the *z*-scores, that is, the scaled probability of observing a visit between a given visitor group and protected areas of given status, calculated as follows $z_{kj} = \frac{v^*_{kj} - \overline{v^*_{.j}}}{\sigma_{v^*_{.j}}}$, where v^*_{kj} is the probability of visit between visitor group *k* and a place with protection status *j*, $\overline{v^*_{.j}}$ is the mean probability of a visit to a place with protection status *j* calculated across all visitor groups, and $\sigma_{v^*_{.j}}$ is the standard deviation across all visitor groups.

We assumed that visitors travelling predominantly to protected areas of high legal protection status (protection status 4 and 5) present low risk whereas visitors travelling predominantly to protected areas of low protection status present high risks. This is because in protected areas of high protection status—areas whereby biodiversity are highly protected and high amount of management programs are carried out (Manaaki Whenua–Landcare Research, 2017; Rutledge et al., 2004)—one can assume that visitors are less likely to encounter exotic species and therefore spread them. Conversely, in areas of low protection status—areas within which

biodiversity protection is of low priority and high amounts of recreational activities are carried out—one can assume that visitors are more likely to encounter exotic species and therefore spread them around. Since we lack information on the direction of the visitors' travelling patterns, we assume that visitor groups that travel to a mixture of both areas present a moderate risk. That said, a visitor moving from a location of low protection status to one of high protection status undoubtedly presents a greater risk that the opposite scenario.

2.3.3 | Assessing predicted areas potentially at risk of visitor-mediated dispersal

To verify whether or not the potential areas of spread identified by the MMSBM parameters of different visitor groups actually correspond to hot spots of potential spread of exotic species across New Zealand, we would require extensive spatial and temporal data on the distribution of exotic species across the country. Unfortunately, such comprehensive data are often not available due to limited sampling effort, unstandardised sampling protocols or biased sampling towards easily accessible sampling sites (Dennis & Thomas, 2000; Howell & Terry, 2016; Kadmon et al., 2004). On the other hand, occurrence data of exotic species are often readily available, in New Zealand and worldwide. We therefore show here how one can use occurrence data in combination with findings from this study to assess the potential risks of visitor-mediated dispersal.

We specifically use occurrence data of exotic plant species extracted from the Bioweb (Howell & Terry, 2016) and the Operational Weeds Application obtained from inventories of pest plants in managed reserves by the Department of Conservation (C. Howell, personal communication, 25 May 2020). To identify which species could potentially be dispersed by visitors, we used the list of the top 30 priority pest plants identified by Auckland Regional Council (Table S9—defined according to the Regional Pest Management Plan 2019–2029; Auckland Regional Council, 2019). However, as this list of pest plants is identified based on the level of environmental threats these species posed or are likely to pose within the regional parks, they might not all be potentially spread by visitors (Auckland Regional Council, 2019). We therefore also used the criteria identified by (Pickering & Mount, 2010), where annual or perennial herbs and graminoids are considered more likely to be dispersed due to their adhesive traits and size—that is, they are more likely to accidentally be dispersed via the visitors' clothes, walking boots and soil movements. Following this, we identified: *Cortaderia jubata*, *Aristea ecklonii*, *Banksia integrifolia*, *Lilium formosanum*, *Anredera cordifolia*, *Cortadaria selloana* as the main exotic species likely to dispersed by visitors (CABI, 2020). However, we only include *Cortaderia jubata* as a case example in the main text but refer to the Supporting Information for the distribution of all the listed exotic species (Figure S5).

Using the MMSBM fits, we then mapped the characterised travelling patterns of the different visitor groups travelling to different regions (or territories) across New Zealand. We then visually compared the distribution of *Cortaderia jubata* to the characterised travelling patterns of the different visitor groups. Based on the relative probability of different visitor groups (or *z*-scores) to travel to different regions (or territories), we then identified the extent to which these different visitor groups matched the distribution of exotic species across the country. For instance though two groups might be travelling to the same region (or territory), we can identify that one visitor group might be dispersing much more than another group based on their relative probability of travelling to that given region.

3 | RESULTS

Based on the BIC scores of the MMSBM fits, we found support for $K = 10$ groups of visitors and $L = 12$ groups of places at the coarser regional scale; and $K = 6$ groups of visitors and $L = 6$ groups of places at the finer territorial scale (Tables S4 and S5). Following the identification of optimal visitor groups (K) and place groups (L), we wanted to further understand whether or not the nodes—that is, visitors and places—within the respective groups followed any particular pattern which would give us an overview of how people travelled across New Zealand. At both spatial scales, we found variation in the way both visitors and places belonged to different groups. For instance, we found that a handful of regions or territories belong predominantly to few place groups (Figure 2). On the other hand, some regions or territories tend to be spread homogeneously across the different place groups (Figure 2). We found no obvious clustering between places from the North and the South Islands of New Zealand at either spatial scales (Figure S4). Similar trends are also observed for visitors. Note that due to the high number of visitors, here we only show the groupings of 100 representative visitors. (Figure 3).

To better characterise travelling patterns of visitor groups to place groups across New Zealand, we used the probability matrix p estimated by the MMSBM. At both spatial scales, we observed that visitors from all visitor groups predominantly travel to certain place groups. On average, at the regional scale, we found that most visitors from the different groups tend to travel predominantly to places within group 1 (mean = 0.662) and group 3 (mean = 0.448) which comprise Auckland (17), Southland (11), Wellington (12), Waikato (16) and Bay of Plenty (15) Regional Councils (Figures 2 and 4; Table S2). At the territorial scale, all visitors on average tend to preferentially travel to places within place group 5 (mean = 0.408) which comprise local Territorial Authorities such as Auckland (21), Queenstown-Lakes District (2), Christchurch City (1), Wellington City (3) and Westland (6) (Figures 2 and 4; Table S3).

When further assessing the likelihood of travelling to protected areas (Figure 5), we found that at both spatial scales, visitor groups are expected to travel predominantly to place groups characterised as protected areas of high protection status (mean = 0.086 at protection status 4; mean = 0.077 at protection status 3) rather than protected areas of lower protection status (mean = 0.001 at areas

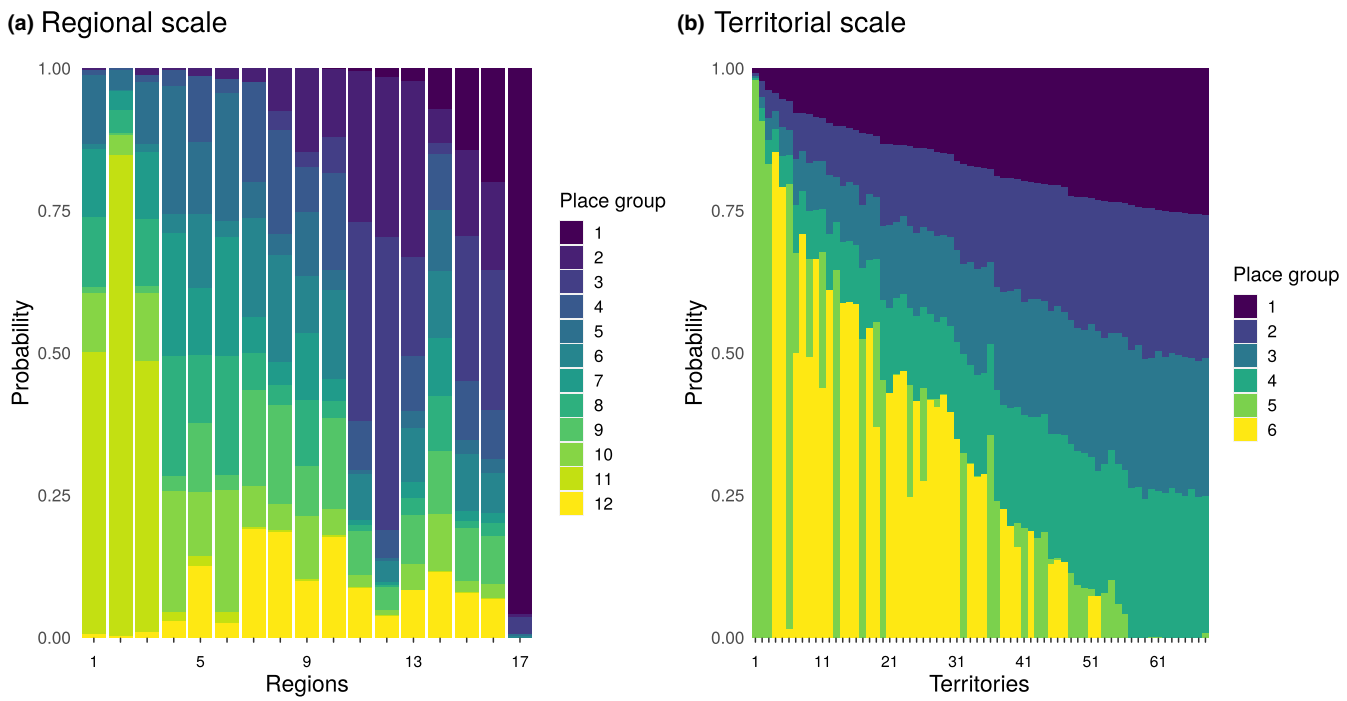

FIGURE 2 Characteristic place groups at the (a) Regional Council and (b) Territorial Authority scales. Each vertical bar refers to a region or territory. At the regional scale, the 17 Regional Councils are numbered from 1 to 17; at the territorial scale, the 68 Territorial Authorities are numbered from 1 to 68 (refer to Tables S2 and S3 for the corresponding Regional Council/Territorial Authority assigned to the different numbers). Each colour represents a place group. Values show the average likelihood each region or territory belongs to each of the different place groups identified by our model. For instance, at the regional scale, region 1 (Area Outside Regional Council) belongs predominantly group 11 and region 11 (Southland Regional Council) is more evenly spread across all 12 place groups. At the territorial scale, territory 1 (Area Outside Territorial Authority) belongs predominantly to place group 5 whereas territory 24 (Clutha District) is more evenly spread across the 6 place groups

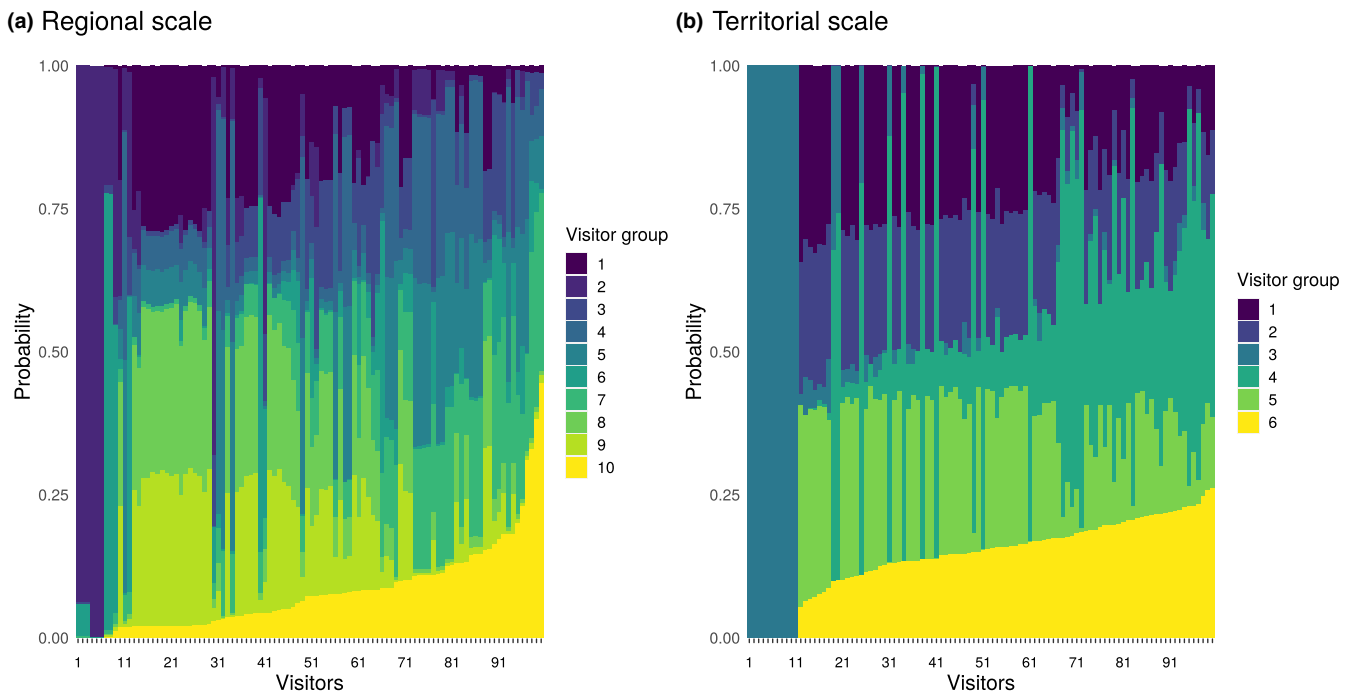

FIGURE 3 Characteristic visitor groups of 100 representative visitors (out of 213,484 total) at the (a) Regional Council and (b) Territorial Authority scales. Each vertical bar refers to a visitor. Each colour represents a visitor group identified by our model. Values show the likelihood for each visitor to belong to each of the different visitor groups. For instance, at the Territorial Scale, visitor 1 belong only to group 2 whereas visitor 49 belongs to a mixture of the six groups

of protection status 1). In addition, relative differences in the travelling patterns were also observed across visitor groups at both spatial scales. For example, visitor group 10 is estimated to predominantly travel to protected areas of low protection status compared to visitor group 3 which tends to travel more homogenously across protected areas of different status (Figure 5).

Since relative differences in the travelling patterns are observed across visitor groups (Figures 4 and 5), the likelihood of visitor-mediated dispersal of exotic species is expected to be different across visitor groups. As such, one could expect that visitor group 10 is more likely to potentially impact protected areas on average compared to visitor group 3 at the regional scale. Based on the distribution

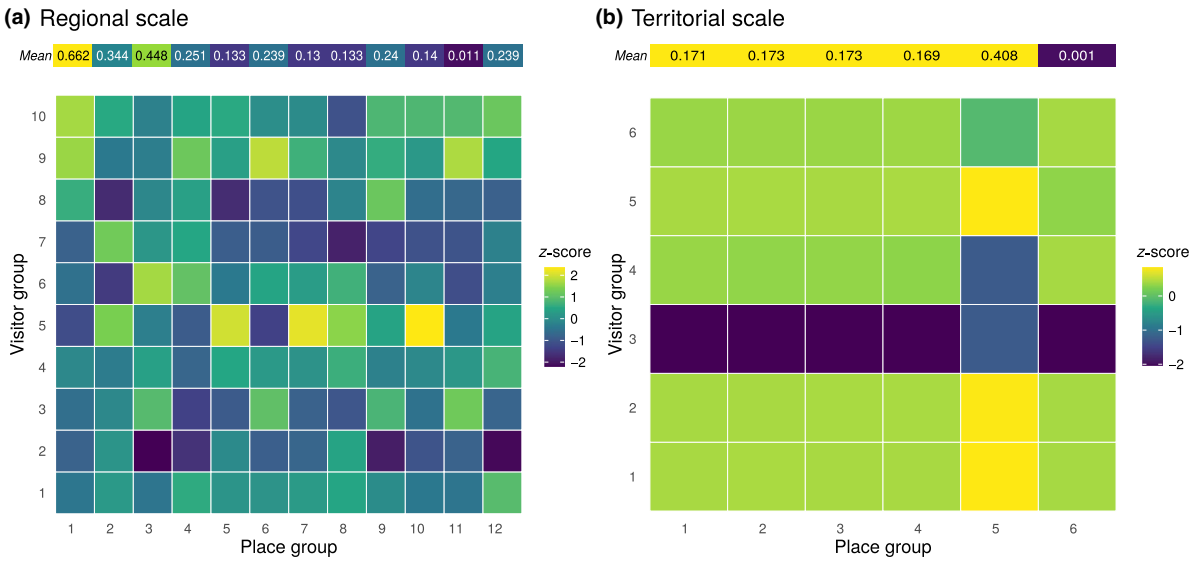

FIGURE 4 Travelling patterns of visitor groups across New Zealand at the (a) Regional Council and (b) Territorial Authority scales. The rows and columns correspond to the visitor groups and place groups, respectively. Values indicate the *z*-scores. Positive values—defined by the colour gradient between green to yellow—indicate a positive deviation from the mean of visit across all visitor groups; negative values—depicted by the colour gradient between purple to blue—indicate a negative deviation from the population mean visits across visitor groups. For example, at the regional scale, visitor group 6 tends to predominantly visit place group 3—which is indicated by a large positive deviation from the population mean—whereas visitor group 2 tends to travel less to place group 3 compared to other visitor groups within the population (e.g. visitor group 6)

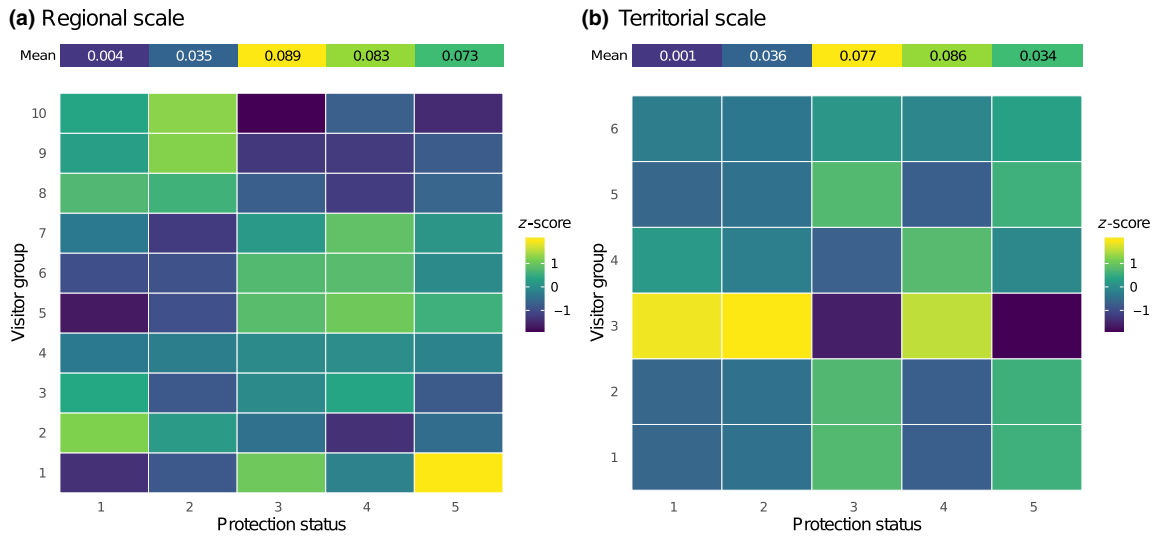

FIGURE 5 Travelling patterns of visitor groups across protected areas in New Zealand at the (a) Regional Council and (b) Territorial Authority scales. The rows and columns correspond to the visitor groups and place groups, respectively. Here, the place groups are characterised as protected areas of different protection status—varying from 1 to 5. Values indicate the *z*-scores, positive values—defined by the colour gradient between green to yellow—indicate a positive standard deviation from the mean of visit across all visitor groups; negative values—depicted by the colour gradient between purple to blue—indicate a negative deviation from the population mean visits across visitor groups

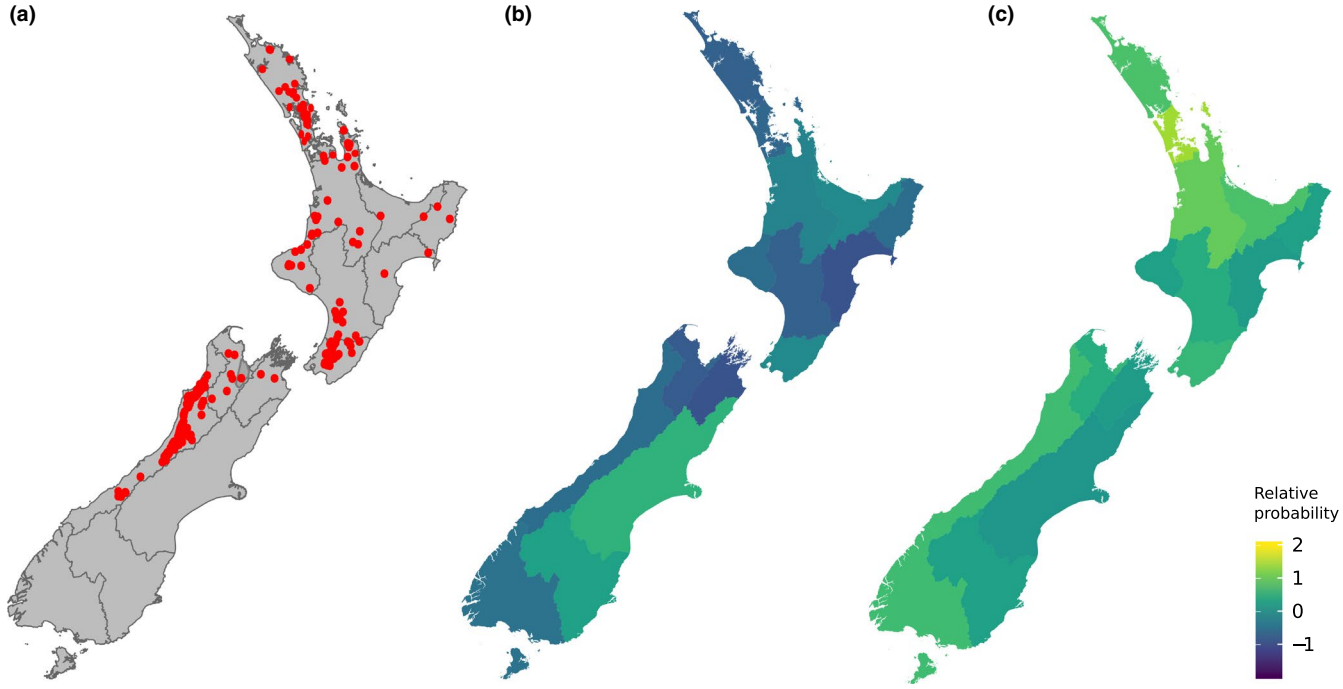

FIGURE 6 Identifying potential areas of visitor-mediated dispersal at the regional scale. (a) New Zealand map showing the occurrence data of the exotic species *Cortaderia jubata*. The data presented here was extracted from inventories of pest plants in managed reserves by the Department of Conservation; (b) Characteristic travelling pattern of visitor group 3 to protected areas projected at the regional scale. (c) Characteristic travelling pattern of visitor group 10 to protected areas projected at the regional scale. Values indicate the relative probability of visiting a particular area. Positive values—defined by the colour gradient between green to yellow—indicate a positive deviation from the mean of visit across all visitor groups; negative values—depicted by the colour gradient between purple to blue—indicate a negative deviation from the population mean visits across visitor groups. Based on the occurrence data, areas such as West Coast, Nelson and Tasman regions correspond to areas with highest occurrence of the exotic species, which correspond to the areas where visitor group 10 tend to predominantly travel to compared to visitor 3

of *Cortaderia jubata*, areas such as West Coast (10), Nelson (7) and Tasman (6) regions correspond to areas with the highest occurrence of this exotic species. Interestingly, the aforementioned areas also correspond to areas predominantly visited by visitor group 10 compared to visitor group 3. Hence, one could expect that visitor group 10 might be contributing more to the dispersal of exotic species compared to visitor group 3. As such, though no occurrence of *Cortaderia jubata* has been reported yet in Canterbury (14) and Southland (11) region, one could expect the Southland region to potentially be affected by visitor-mediated dispersal in the near future (Figure 6).

4 | DISCUSSION

In our study, we have treated visitor's travelling patterns as a proxy of propagule pressure to assess the potential contribution of unintended visitor-mediated dispersal. The characterised travelling patterns of visitors across New Zealand indicate that both visitors and places can be grouped based on the similarity of their visitor–place interactions at both regional and territorial scales. Though all visitor groups predominantly travelled to some common place groups at both the regional and territorial scales, we also observed important variation in the travelling patterns across visitor groups. When focusing on the travelling patterns of visitors to protected areas, we found that visitors tend to travel predominantly to areas of high legal protection status at both spatial scales. Our results highlight the heterogeneity of the visitors' travelling patterns. From a risk assessment point of view, this is important as it implies that visitors travelling across New Zealand might not all contribute to the dispersal of exotic species to the same extent. In doing so, our study highlights the importance of incorporating and understanding human behaviour when assessing human-mediated dispersal—especially when the identity of the target exotic species and/or the dispersal routes are unknown.

To our knowledge, limited studies have focused on understanding the vectors' behaviour to assess their relative risks in dispersing exotic species (Anderson et al., 2014; Chan et al., 2013; Kaluza et al., 2010). Rather than using traditional risk assessment methods—focused around the introduced/invasive species (Kolar & Lodge, 2002; Pheloung et al., 1999), we propose instead to focus on the vectors—that is, monitoring of individuals or species acting as dispersers as suggested in various studies (Andow, 2003; Hulme, 2009). To do so, we suggest using a MMSBM approach, as it can provide an overview of the dispersal routes of the vector—which can improve our understanding of the roles played by the dispersal vector while also identifying the potential areas at risk. As a result, the MMSBM represents a flexible approach to understand broad-scale patterns of human-mediated dispersal of exotic species.

Categorising visitors into distinct groups is quite common when attempting to get an overview of behavioural patterns (Eiswerth et al., 2001; Moore et al., 2012). However, here we showed that based solely on the similarity of visitor–place interactions, visitors can be robustly categorised into groups at both spatial scales. Moreover, we found that both visitors and places belonged to a mixture of groups, with relative differences in their 'typical' ways they travel across the country. Despite the relative differences observed in the visitors' travelling patterns, we also found that visitors across all groups tended to travel predominantly to certain place groups which correspond to places which are either popular and/or with high accessibility. When further estimating the likelihood for visitors to travel to protected areas at both spatial scales, similar observations were also found. Visitors are more likely to travel to protected areas with higher legal protection status—which correspond to protected areas with a high number of conservation and management projects, but also higher accessibility to visitors (Manaaki Whenua–Landcare Research, 2017; Rutledge et al., 2004). This supports previous work which identified high abundances of exotic species around trails, tracks and recreational areas in New Zealand (Mack et al., 2000; McNeill et al., 2011), and a high invasive species richness in protected areas having a higher accessibility (Gallardo et al., 2017).

As resources are often limited for management purposes, results from this study could potentially be used as a baseline study to identify the relative risk of the different visitor groups and places which may require further investigation and surveillance. As a representative example in Figure 6, we showed that by combining our results, occurrence data of exotic species and the level of different protection status assigned to protected areas as a proxy of the level of management in these areas (Rutledge et al., 2004), one could use the MMSBM approach to potentially identify which visitor group might be contributing the most to the dispersal of exotic species. We can similarly identify areas which could potentially be impacted the most in the future. As a consequence, these areas could be targeted by practitioners for further monitoring and surveillance.

Note, however, that our results only provide an approximate means to quantify the likely impacts of visitors in the spread of introduced species both across New Zealand and at the level of protected areas at the regional and territorial scale. In the current analysis, we assumed that each region (or territory) was equally likely to be visited when assessing the likelihood of visitor-mediated dispersal of exotic species to protected areas. Though this does not impact the fits of the MMSBM, it does represent a particularly strong assumption about visitor behaviour. If finer scale visitation data (i.e. at the level of protected areas) were available, this assumption should be adjusted by using the weighted probability of visiting the specific protected areas within the respective regions to increase the accuracy of our results. In addition, though the MMSBM approach presented here allowed us to identify characteristic groups of visitors and places, it currently does not allow us to predict dynamics of visitor–place interactions. This is particularly important when assessing and identifying potential areas which might be impacted by visitor-mediated dispersal, especially in the case of protected areas. For example, the construction of roads and tracks to increase the accessibility to remote areas within national parks; or the increasing popularity of particular places due to social media can influence the visitors' behaviour in travelling across the country (Doscher et al., 2011; Miller et al., 2019; Moore et al., 2012), hence affecting the potential dispersal of exotic species.

In an ideal world, we would also have temporal and spatially replicated field data as in Dauer et al. (2007) and including soil and vegetation sampling along the visitation network as in Pickering et al. (2011) to further validate the predictions and hypotheses proposed in the current study. Such empirical data would enable us to test whether the potential hotspots of invasion and likely hubs identified in the current study could generate further spread of exotic species through the network. However, one should also consider other nature-based tourism associated activities which might also be affecting the dispersal of exotic species. For instance, vehicles which might also be introducing species during the construction of tracks and roads in the vicinity of protected areas (Ansong & Pickering, 2013; Clifford, 1959; Lonsdale & Lane, 1994; Pickering & Mount, 2010); disturbance induced by vegetation clearance; soil erosion and compaction induced by camping and tramping, internal fragmentation by use of non-formal trails might all be contributing to the presence of exotic species (Barros & Pickering, 2015; Barros et al., 2015; Leung & Marion, 1996; Monz et al., 2010). Likewise, just because a vector *could* potentially spread an exotic species does not imply that it will be able to successfully establish, as it will also depend on the recipient community's environmental and climatic conditions. Though including these features is beyond this study, they would seem like particularly valuable additions going forward.

From a visitor-mediated dispersal point of view, identifying how visitors travel alone sets an important, if admittedly incomplete, baseline for the likelihood visitors actually impact the places they visit. As a key step moving forward, factors such as the: (a) order of places to which visitors travel, (b) number of visitors taking different paths and (c) the time visitors spend at each location should be included in future studies. These factors are crucial to assess the level of risk a particular visitor group might be posing in dispersing exotic species (Auffret et al., 2014; Chown et al., 2012; Wichmann et al., 2009; Wilson et al., 2009). Unfortunately, the surveys we accessed lack information about the directionality of the visitors' travelling patterns. In the future, a small but consequential change would be for surveyors to collect information about the next place that visitors intend to go in addition to a list of where they have been. By providing this finer-scale information, it could enable us to assess the relative risk of visitors in spreading exotic species when they travel more accurately. As noted previously, the distinction between a visitor travelling from a protected area of higher to a lower protection status and a visitor travelling from a protected area of lower to a higher protected area is ecologically crucial. In the first case, one could suspect that the visitor would of lower risk of disseminating exotic species whereas in the second case the visitor could be suspected to be of higher risk.

Though in the current study we only present on visitor-mediated dispersal of exotic species within New Zealand, the MMSBM presented here is generalisable and could be applied to

data from other systems—especially in cases where neither the dispersal route nor the focal exotic species are known but where data about the vector are more plentiful. By doing so, this could potentially help practitioners to identify areas which might require further monitoring and management—thereby reducing the associated costs to the management of exotic species (Finnoff et al., 2007; Kaiser & Burnett, 2010; Kean et al., 2008). As such, the use of network models as presented in this study could be beneficial to improve multiple risk-assessment procedures.

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AUTHORS' CONTRIBUTIONS

R.R. and D.B.S. designed the study; R.R., B.B.M. and A.G.-L. contributed to the code; R.R. carried out the analysis and wrote the first draft of the manuscript. All authors contributed to framing the manuscript, editing and approving the final draft.

DATA AVAILABILITY STATEMENT

All visitation data from the Ministry of Business Innovation & Employment (MBIE) used in this study are publicly available on https://www.mbie.govt.nz/ and data from the National Survey of New Zealander is provided upon request by the Department of Conservation (DOC). Data on the layers from Protected Area Network New Zealand were provided upon request by Manaaki Whenua–Landcare Research. Data on the distribution of exotic pest plants were extracted from two Department of Conservation (DOC) databases: BioWeb and the Operational Weeds Application which were accessed on 25 May 2020 (C. Howell, pers. comm.) by Clayson Howell. All codes used in the current study are available at https://github.com/rogini98/MMSBM_visitation_network.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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