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Using niche conservatism information to prioritize hotspots of invasion by non-native freshwater invertebrates in New Zealand

Ursula Torres[1] | William Godsoe[1] | Hannah L. Buckley[2] | Matthew Parry[3] | Audrey Lustig[4] | Susan P. Worner[1]

[1]Bio-protection Research Centre, Lincoln University, Canterbury, New Zealand

[2]Auckland University of Technology, Auckland, New Zealand

[3]Department of Mathematics & Statistics, University of Otago, Dunedin, New Zealand

[4]Te Pūnaha Matatini and the Geospatial Research Institute, University of Canterbury, Christchurch, New Zealand

Correspondence
Ursula Torres, Bio-protection Research Centre, Lincoln University, PO Box 85084, Canterbury 7647, New Zealand.
Email: ursula.torres.m@gmail.com

Present address
Ursula Torres, Ministry for Primary Industries, PO Box 2526, Wellington, 6140, New Zealand.

Abstract

Aim: Identifying suitable areas for invasive species establishment is of critical importance for their early detection and rapid eradication. However, our ability to detect suitable areas is impeded by the tendency of species to shift their niche postinvasion. In this study, we (a) investigate the frequency of niche shift within invasive freshwater invertebrates and (b) use niche conservatism information to prioritize potential hotspots of invasion for non-native freshwater invertebrates in New Zealand.

Location: Global occurrence data and predictions over New Zealand.

Methods: We characterized the native and invasive realized niche using occurrence data for 22 invasive freshwater invertebrates in relation to 27 derived climate variables. Using principal component analysis and species distribution models, we measured the degree of niche shift for each species and identified hotspots of invasion and niche conservatism described within biogeographic units in New Zealand.

Results: Niche shift was detected frequently among the invasive freshwater invertebrates studied here, where 90% showed a significant niche change. The characterization of the species niche enabled the identification of species whose management might be hampered because of their ability to colonize novel environments. Locations covering more than half of the land area of New Zealand were found to be climatically suitable for at least four and up to 11 species. Areas that were found to be climatically suitable for several species but were not identified as hotspots of niche conservatism could be considered less critical for surveillance and monitoring.

Main conclusions: Aquatic invertebrates show a high degree of niche shift. By combining climate suitability predictions and niche conservatism, we were able to prioritize invasion areas.

KEYWORDS
biogeographic units, hotspots of invasion, invasive freshwater invertebrates, niche conservatism, niche shift, species distribution models

1 | INTRODUCTION

Biological invasions represent one of the major threats to biodiversity (Gurevitch & Padilla, 2004). Furthermore, other human-driven components of global change, such as climate change and habitat fragmentation, are predicted to increase the prevalence and range of invasive species worldwide (Dukes & Mooney, 1999; Walther et al., 2009). Early detection followed by a rapid control response can have considerable influence on a successful eradication of an introduced species (Myers, Simberloff, Kuris, & Carey, 2000). Therefore, identifying the environments where an introduced species is likely to thrive is of critical importance for detecting areas where surveillance, containment or eradication need to be applied. Surveillance strategies are usually species specific and are focused on economic optimization and detection maximization (Dodd, McCarthy, Ainsworth, & Burgman, 2016); however, assessing the risk of invasion for multiple species in an area should facilitate the development of more cost-effective and targeted management strategies (Gallardo & Aldridge, 2013). Also known as hotspot analysis, this approach to the detection of suitable environments for multiple species is traditionally used to identify high biodiversity areas, but has been also applied to detect hotspots of biological invasions (e.g., Adhikari, Tiwary, & Barik, 2015; O'Donnell et al., 2012). Hotspots of biological invasions can be described within biogeographic regions that encompass a distinctive set of communities with similar environmental conditions, disturbance regimes and natural barriers. Because these communities function together, an assessment of the risk of invasion by biogeographic region is likely going to facilitate management strategies. However, one remaining challenge is to adequately identify hotspots of invasion and prioritize those areas when resources are limited.

Several studies report the dramatic increase in non-native freshwater invertebrates arrival and/or establishment in different regions of the world (Devin, Bollache, Noël, & Beisel, 2005; Robinson, 1999; Roy et al., 2014). While New Zealand freshwater ecosystems have not been an exception to this trend, they have been mainly affected by purposeful introductions of non-native species for recreational activities and aquaculture (e.g., Townsend, 1996). However more recently, many introductions of invertebrates have been unintentional, highlighting the importance of implementing effective surveillance strategies by identifying potential establishment areas (e.g., Collier, Demetras, Duggan, & Johnston, 2011; Duggan, 2002; Duggan, Green, & Burger, 2006; Duggan, Neale, Robinson, Verburg, & Watson, 2014; Holder et al., 2010; Rowe, Davies, Pohe, & Simpson, 2011). Correlative species distribution models (SDMs) are statistical models used to identify potential suitable environments for species, by associating their occurrence with the prevailing environmental factors at those locations (Elith et al., 2006; Guisan & Thuiller, 2005). In general, SDMs are based on theories developed by Hutchinson (1957), where a species niche describes the combination of environments required to support a persistent population and is represented by a hypervolume of those environmental conditions. In practice, correlative SDMs capture only a portion of the fundamental niche, described as the realized niche which encompasses the environmental conditions to which a species is confined, due to interactions with other species and dispersal restrictions (Hutchinson, 1957; Pulliam, 2000).

Using SDMs to predict species invasion probabilities into other areas relies on the assumption of niche conservatism that requires that the realized niche is conserved between the native and invaded ranges (Peterson, Soberón, & Sánchez-Cordero, 1999; Wiens & Graham, 2005). However, not all invasive species necessarily retain their environmental requirements from the native range, such that any change in the position or the limits of the niche envelope indicates a realized niche shift (Guisan, Petitpierre, Broennimann, Daehler, & Kueffer, 2014). A shift in the realized niche can be the result of adaptive evolution in the new range (Lounibos, Escher, & Lourenço-De-Oliveira, 2003) or from changes in biotic interactions, from dispersal constraints or from preadaptation to conditions that were previously available in the native range (Guisan et al., 2014). In fact, niche shifts have been reported across a broad range of taxa such as terrestrial plants, reptiles, amphibians, birds, insects and marine fish (Hill, Gallardo, & Terblanche, 2017; Li, Liu, Li, Petitpierre, & Guisan, 2014; Parravicini, Azzurro, Kulbicki, & Belmaker, 2015; Petitpierre et al., 2012; Strubbe, Broennimann, Chiron, & Matthysen, 2013). While the tendency to niche shifts has been extensively investigated for terrestrial organisms, little is known about aquatic species. For invasive freshwater invertebrates, in particular, most studies of niche shifts are based on a small number of species (e.g., Capinha, Leung, & Anastácio, 2011; Gallardo, zu Ermgassen, & Aldridge, 2013; Larson & Olden, 2012; Medley, 2010; Morehouse & Tobler, 2013); thus, a general trend for this group of species has yet to be determined.

It is therefore critical to detect when niche shifts occur from a fundamental perspective for invasion ecology but also to identify invasive species that are likely to pose problems for management because of their ability to colonize novel environments. In the context of invasion, if the species conserves the environmental preferences of their native range, a SDM should correctly identify suitable areas in the non-native range, and therefore, priority areas for monitoring can be easily identified. But if a niche shift has occurred, the invader's potential habitats should be considered carefully as it can establish in environments not occupied in the native range, making it difficult to prioritize areas and therefore hampering its management. Niche shifts can be observed in analogous (environments present in both invaded and native ranges) and/or nonanalogous environments (environments present only in one range) (Guisan et al., 2014). A much debated question is how to interpret niche shifts in nonanalogous environments (Guisan et al., 2012; Webber et al., 2012); nevertheless, their identification will also be of importance from a management perspective. In addition, information about niche conservatism is also likely to be important to consider for prioritization of surveillance areas in a target region. By identifying environments where species show niche conservatism, areas more likely to be colonized by the species can be determined because these environments may represent optimal conditions for the species establishment.

In this study, we investigate the prevalence of climatic niche shifts in invasive freshwater invertebrates and how that information could be used in the identification of invasion risk areas. Using the distribution of 22 globally invasive freshwater species, we compare the native and invasive niche to estimate for the first time the frequency of occurrence of climatic niche shifts for freshwater invertebrates. We use nine correlative SDMs to identify hotspots of invasion in New Zealand. The hotspots of invasion were described within biogeographic regions, and we apply a novel approach to prioritize invasion risk areas by combining information about niche conservatism and climate suitability. The specific objectives were to (a) determine whether invasive freshwater invertebrates have changed their native climatic niche during invasion across the world in both analogous and nonanalogous environments and (b) identify and prioritize potential hotspots of invasion for target species in New Zealand.

2 | METHODS

2.1 | Target species and occurrence data

Twenty-two invasive freshwater species from around the world were selected for this study (Table 1). These species are known to cause considerable impact in several regions (Loo, 2012; Smith & Dodgshun, 2008). The distribution information for the 22 species was extracted from GBIF (www.gbif.org, last accessed 5 May 2014)

TABLE 1 List of species studied, their number of occurrences and respective native range

Class	Family	Full name	Number of occurrences	Native range
Insecta	Culicidae	*Aedes albopictus* (Skuse, 1895)	2,940	Asia
Gastropoda	Bithyniidae	*Bithynia tentaculata* (Linnaeus, 1758)	1,040	Europe
Branchiopoda	Cercopagididae	*Bythotrephes longimanus* (Leydig, 1860)	519	Europe and Asia
Branchiopoda	Cercopagididae	*Cercopagis pengoi* (Ostroumov, 1891)	151	Ponto Caspian countries[a]
Gastropoda	Viviparidae	*Cipangopaludina japonica* (von Martens, 1861)	51	Asia
Bivalvia	Corbiculidae	*Corbicula fluminea* (O. F. Müller, 1774)	1,874	Asia
Malacostraca	Gammaridae	*Dikerogammarus villosus* (Sowinsky, 1894)	91	Ponto Caspian countries
Bivalvia	Dreissenidae	*Dreissena rostriformis bugensis* (Andrusov, 1897)	239	Dnieper Delta countries[b]
Bivalvia	Dreissenidae	*Dreissena polymorpha* (Pallas, 1771)	1,498	Ponto Caspian countries
Malacostraca	Varunidae	*Eriocheir sinensis* (Milne-Edwards, 1854)	1,106	Asia
Malacostraca	Gammaridae	*Gammarus tigrinus* (Sexton, 1939)	287	North America
Malacostraca	Mysidae	*Hemimysis anomala* (G.O. Sars, 1907)	95	Ponto Caspian countries
Bivalvia	Mytilidae	*Limnoperna fortunei* (Dunker, 1857)	118	Asia
Malacostraca	Cambaridae	*Orconectes limosus* (Rafinesque, 1817)	881	North America
Malacostraca	Cambaridae	*Orconectes virilis* (Hagen, 1870)	557	North America
Malacostraca	Astacidae	*Pacifastacus leniusculus* (Dana, 1852)	545	North America
Gastropoda	Ampullariidae	*Pomacea canaliculata* (Lamarck, 1828)	227	South America
Gastropoda	Tateidae	*Potamopyrgus antipodarum* (Gray, 1843)	1,872	New Zealand
Malacostraca	Cambaridae	*Procambarus clarkii* (Girard, 1852)	499	North America
Hexanauplia	Pseudodiaptomidae	*Pseudodiaptomus inopinus* (Burckhardt, 1913)	35	Asia
Malacostraca	Panopeidae	*Rhithropanopeus harrisii* (Gould, 1841)	138	East Coast of North America
Gastropoda	Valvatidae	*Valvata piscinalis* (Muller, 1774)	996	Europe

Note. References for the native range can be found in Supporting information Appendix S13.
[a]Ponto Caspian countries comprise the Russian Federation, Ukraine, Romania, Bulgaria, Kazakhstan, Uzbekistan, Turkmenistan, Tajikistan, Kyrgyzstan, Iran, Georgia and Azerbaijan. [b]Dnieper Delta countries comprise the Russian Federation, Ukraine and Belarus.

and GISIN (www.niiss.org, last accessed 18 December 2014) and collected from publications and taxon experts (for further details, see Worner, Ikeda, Leday, and Joy (2010)). The native and invaded range status for each species was delimited by country or continent (Table 1). Occurrence maps can be found in Appendix S1 in Supporting Information. The resolution for extracting environmental information was set to 10 arc min (0.17°), and only one occurrence point per grid cell was used to minimize spatial autocorrelation and inflation of accuracy measures (Kramer-Schadt et al., 2013; Veloz, 2009).

2.2 | Climatic data

Twenty-seven climatic variables associated with temperature, radiation and precipitation were extracted from Climond (Kriticos et al., 2012) at 10 arc min (0.17°) resolution to characterize each occurrence point (Table 2). At the global scale, only air temperature was available; however, using this variable to represent conditions in freshwater ecosystems is customary (Lauzeral et al., 2011), particularly for well-mixed water bodies such as river and streams where a high positive correlation has been found between air and water temperature (Caissie, 2006).

2.3 | Geographic background for niche comparison and species distribution models

In addition to extracting climatic conditions from locations where the species were known to be present, the climatic conditions of the geographic background were also extracted. The geographic background is the study area limited to the available environments that each species could colonize and to which species distribution models are usually calibrated (Peterson, 2011). To delimit the geographic background for niche comparison, we used freshwater ecoregions defined by Abell et al. (2008) that overlapped with the native and invaded distributions. The purpose was to delimit an area where each species would naturally disperse as recommended by Peterson (2011). In general, freshwater organism dispersal is limited by the continuity of water bodies, and freshwater ecoregions reflect these natural barriers.

Because true absence data are often not available to calibrate SDMs, pseudo-absences are generated in the geographic background. We used a different criterion to delimit the geographic background to calibrate SDMs, because small changes in the geographic background can significantly affect the model performance (VanDerWal, Shoo, Graham, & Williams, 2009). As the geographic background increases, the correlation structure between environmental variables is likely to change, which can negatively affect model performance (Dormann et al., 2013). Thus, we used a more restrictive criterion developed by Senay, Worner, and Ikeda (2013) that enables to delimit a geographic background with similar correlation structures between environmental variables. To find the appropriate distance to delimit the geographic background for each species, twenty datasets that included 27 climatic variables from Climond

were extracted using different radii from the presence points (every 50 km from 50 to 1,000 km). For each radius, we used principal component analysis (PCA) to measure the changes in variable loading across changes in distance for the variables contributing the most to principal components (Senay et al., 2013). A change in sign in the variable loading indicates that the relationships between variables are different, and therefore, the optimal distance should be where the sign is consistent.

2.4 | Niche analysis

We compared native and invasive niche for each species using the two-first components of a principal component analysis (PCA). Only the two-first components were used to facilitate visualization and computation for the niche metrics (Broennimann et al., 2012). To correct for sample bias and smooth gaps in the climatic niche, a probability density function (PDF) was constructed. The PDF was constructed using a smoothed kernel estimator around scores from the PCA for the environment occupied by the species and the geographic background (Broennimann et al., 2012). Following procedures established by Broennimann et al. (2012), a grid was placed over the entire environmental space to divide it into 100 by 100 cells, creating a unitless raster. The niche changes of each species were characterized using five metrics: niche overlap, niche stability, niche expansion, niche unfilling and centroid change (see Table 3 for definitions, Figure 1 for an illustration of the niche metrics). All metrics vary between 0 and 1; values close to 1 indicate a high overlap, stability, expansion, unfilling or centroid change. Niche equivalency and similarity tests were performed using the niche overlap metric following Broennimann et al. (2012) (Table 3). Two species (*Dikerogammarus villosus* and *Hemimysis anomala*) were excluded from the niche analysis as there were not enough occurrence records in their native range (less than five occurrence points).

We computed the metrics in analogous and in all environments (nonanalogous and analogous environments) to identify in which type of environments niche changes are occurring (Figure 1). Because some climates can be more common in the invaded range than in the native range (or conversely), false niche differentiation can be detected (Godsoe, 2010; Guisan et al., 2014). It is thus important to consider climate availability between the invaded and native ranges when measuring niche changes. Following recommendations by Guisan et al. (2014) for accounting for climate availability, we also computed niche metrics in the most common environments between the invaded and native ranges by removing marginal climates (environments with low probability density). However, removing marginal climates could strongly influence the niche change metrics, so a sensitivity analysis, as recommended by Petitpierre et al. (2012), was carried out to determine whether the metric changes with the degree of removal of marginal climates. A range of six percentiles was used to remove marginal climates in each range, including 75%, 80%, 85%, 90%, 95% and 100%. Two niche metrics within this range of percentiles were compared: niche expansion and unfilling, following Petitpierre et al. (2012).

TABLE 2 Variables extracted from the Climond database (Kriticos et al., 2012)

Code	Variables
CBIO1	Annual Mean Temperature
CBIO2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
CBIO3	Isothermality (CBIO2/CBIO7) (* 100)
CBIO4	Temperature Seasonality (standard deviation *100)
CBIO5	Max Temperature of Warmest Month
CBIO6	Min Temperature of Coldest Month
CBIO7	Temperature Annual Range (CBIO5-CBIO6)
CBIO8	Mean Temperature of Wettest Quarter
CBIO9	Mean Temperature of Driest Quarter
CBIO10	Mean Temperature of Warmest Quarter
CBIO11	Mean Temperature of Coldest Quarter
CBIO12	Annual Precipitation
CBIO13	Precipitation of Wettest Month
CBIO14	Precipitation of Driest Month
CBIO15	Precipitation Seasonality (Coefficient of Variation)
CBIO16	Precipitation of Wettest Quarter
CBIO17	Precipitation of Driest Quarter
CBIO18	Precipitation of Warmest Quarter
CBIO19	Precipitation of Coldest Quarter
CBIO20	Annual mean radiation (W/m^2)
CBIO21	Highest weekly radiation (W/m^2)
CBIO22	Lowest weekly radiation (W/m^2)
CBIO23	Radiation seasonality (C of V)
CBIO24	Radiation of wettest quarter (W/m^2)
CBIO25	Radiation of driest quarter (W/m^2)
CBIO26	Radiation of warmest quarter (W/m^2)
CBIO27	Radiation of coldest quarter (W/m^2)

2.5 | Species distribution models

2.5.1 | Pseudo-absence generation

The pseudo-absences were generated in the previously delimited geographic background, selecting environments that are outside of the realized niche using procedures developed by Worner et al. (2014). Compared to random pseudo-absence generation, this method reduces the chance of introducing false absences or locations with suitable environment that could cause an underestimation of the potential distribution of the species. First, the environments within the geographic background are classified as suitable and unsuitable locations using a one-class support vector machine (OCSVM) algorithm (Schölkopf, Platt, Shawe-Taylor, Smola, & Williamson, 2001). OCSVM assesses dissimilarity between presence locations and other locations. If the observation is too different (zero similarity to presence points), it is labelled as out of class and thus considered as a potential

pseudo-absence. Because there were many thousands of potential pseudo-absences, the final step was to group the unsuitable locations according to their environmental characteristics using a k-means algorithm (Lloyd, 1982) and using the centroids of the k clusters to represent the environment of the unsuitable sites. The number of pseudo-absences (k cluster centroids) obtained was set to the equivalent number of presences for the species (Senay et al., 2013).

2.5.2 | Variable selection for the prediction of species distribution

Variable selection was carried out using random forests (Breiman, 2001), for which the most important advantages are robustness against overfitting, incorporation of predictor interactions and a measure of variable importance (Díaz-Uriarte & Alvarez de Andrés, 2006). Using random forests as a variable selection method was proposed by Díaz-Uriarte and Alvarez de Andrés (2006), where variables are selected based on their importance and minimizing out-of-bag (OOB) error. Variables selected for each species can be found in Supporting information Appendix S4.

2.5.3 | Model selection and parameterization

To model species occurrence, an ensemble approach described by Araújo and New (2007) was used. Such an approach deals with model variability by combining predictions. We used nine models in a multi-model framework (Worner et al., 2014). The models were (a) logistic regression (LOG) (McCullagh & Nelder, 1989), (b) classification and regression trees (CART) (Breiman, Friedman, Stone, & Olshen, 1984), (c) conditional trees (CTREE) (Hothorn, Hornik, & Zeileis, 2006), (d) k-nearest neighbours (KNN) (Altman, 1992), (e) naïve Bayes (NB) (McCallum & Nigam, 1998), (f) support vector machines (SVM) (Cortes & Vapnik, 1995), (g) artificial neural networks (NNET) (Venables & Ripley, 2002), (h) linear discriminant analysis (LDA) (McLachlan, 1992) and (i) quadratic discriminant analysis (QDA) (McLachlan, 1992).

Models were calibrated using both native and invasive distributions. Some algorithms (KNN, SVM and NNET) require prior parameterization; hence, several parameter sets were tested using 10-fold cross-validation repeated 20 times. The parameters that yielded the smallest misclassification error were selected (Leday, 2008). The initial tested parameters and final parameters used for each model and species can be found in Supporting information Appendices S5 and S6, respectively.

A 10-fold cross-validation with 200 repetitions was used to evaluate the average performance of each model using the area under the receiver operator characteristic curve (AUC) (Fielding & Bell, 1997) that has the advantage of being a threshold-independent metric. The predictions of the different models were combined using model averaging weighted by Somers' D where $S = 2 \times (AUC-0.5)$ (Breiner, Guisan, Bergamini, & Nobis, 2015). Accordingly, models that were outstanding in their performance were given a higher weight when calculating the average prediction (see Supporting information Appendix S7 for Somers' D results). In addition, the percentage of correctly predicted presences in the invasive range

TABLE 3 Niche metric definitions

| Niche metric	Definition	References
Niche overlap	Intersection of two niches in the *n*-dimensional environmental space. Niche overlap is computed using occurrence densities established by the smoothed kernel estimator. The calculated overlap also accounts for difference in climate availability between the native and invaded ranges. Details on the computation can be found in Broennimann et al. (2012)	Broennimann et al. (2012), Guisan et al. (2014), Schoener (1970) and Warren, Glor, & Turelli (2008)
Niche stability	Proportion of environments (cells) of the invasive niche shared between the native and invasive niches	Guisan et al. (2014) and Petitpierre et al. (2012)
Niche expansion	Proportion of environments (cells) of the invasive niche that does not intersect with native niche	Guisan et al. (2014) and Petitpierre et al. (2012)
Niche unfilling	Proportion of environments (cells) of the native niche that does not intersect with the invasive niche (i.e., environments not (yet) filled in the invasive range)	Guisan et al. (2014) and Petitpierre et al. (2012)
Centroid change	Euclidean distance between the native and invasive niche centroids compared in relation to the extent of the overall species niche	Further details and a script are given in Supporting information Appendices S2 and S3, respectively

Notes. Niche overlap provides statistical tests of niche equivalency and similarity. Niche equivalency tests whether two niches are equivalent by randomly reassigning occurrences from both invasive and native niches. Niche similarity evaluates whether the invasive niche is more similar to the native niche than expected by chance.

was computed for each model and species (Supporting information Appendix S8). Predictions for New Zealand were carried out using a high-resolution 30-arc second Climond dataset, derived from the 10-arc min Climond dataset by bilinear interpolation. The dataset was obtained from Senay et al. (2013). As SDMs were calibrated using climate data at 10 arc min, predictions in the derived high-resolution climatic layers should not be affected. A comparison of the species distribution predictions at both resolutions showed no major difference in the pattern or configuration except for the better defined edges of distribution predictions in the case of the 30-arc sec dataset (Supporting information Appendix S9). Averaged predictions were transformed to discrete classes (presence and absence) using the prevalence approach (Liu, Berry, Dawson, & Pearson, 2005). The

threshold was set to 0.5 as the prevalence in the current study was 50% for all species. Other threshold approaches could be used to optimize predictions of species distribution; however, at prevalence of 50%, Liu et al. (2005) showed that the performance of different threshold approaches did not differ significantly.

2.5.4 | Hotspots of invasion and niche stability in New Zealand

To obtain hotspots of invasion in New Zealand, the species distributions predicted by SDMs were overlaid. To obtain hotspots of niche stability (i.e., niche conservatism), New Zealand areas that corresponded to climatic niche stability of the potential invasive species
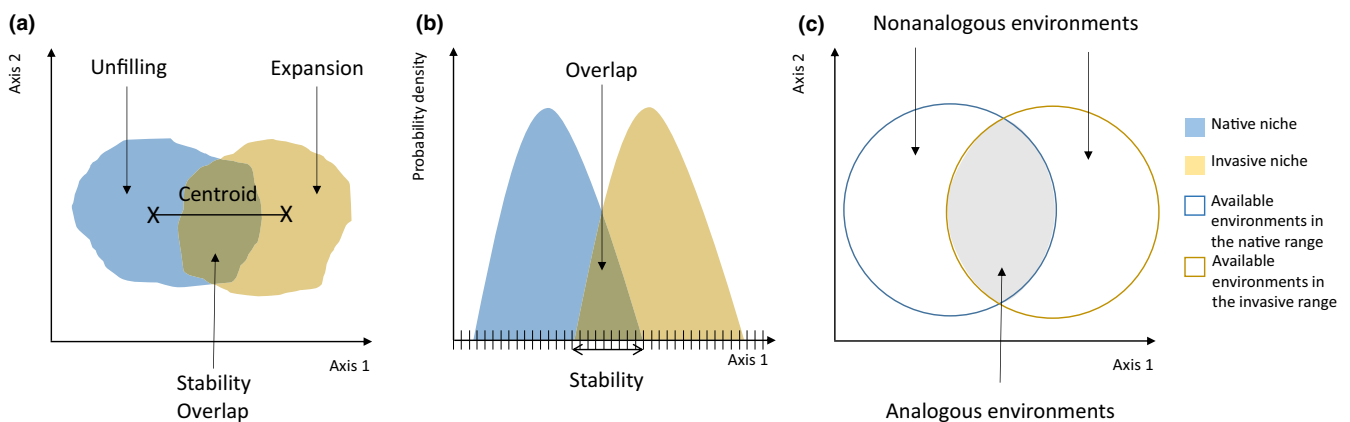
FIGURE 1 (a) Schematic representation of the five niche metrics used to characterize niche changes in two hypothetical climatic axes (see Table 3 for definitions). (b) Simplified schematic representation of niche overlap and stability in one gridded axis. Niche overlap is computed with the occurrence densities established by the smoothed kernel estimator. Niche stability is the proportion of cells of the invasive niche shared between the native and invasive niches. (c) Schematic representation of analogous and nonanalogous environments. The grey area shows environments that are common to both native and invaded ranges (analogous environments), while the white area shows environments existing in only one range (nonanalogous environments) [Colour figure can be viewed at wileyonlinelibrary.com]
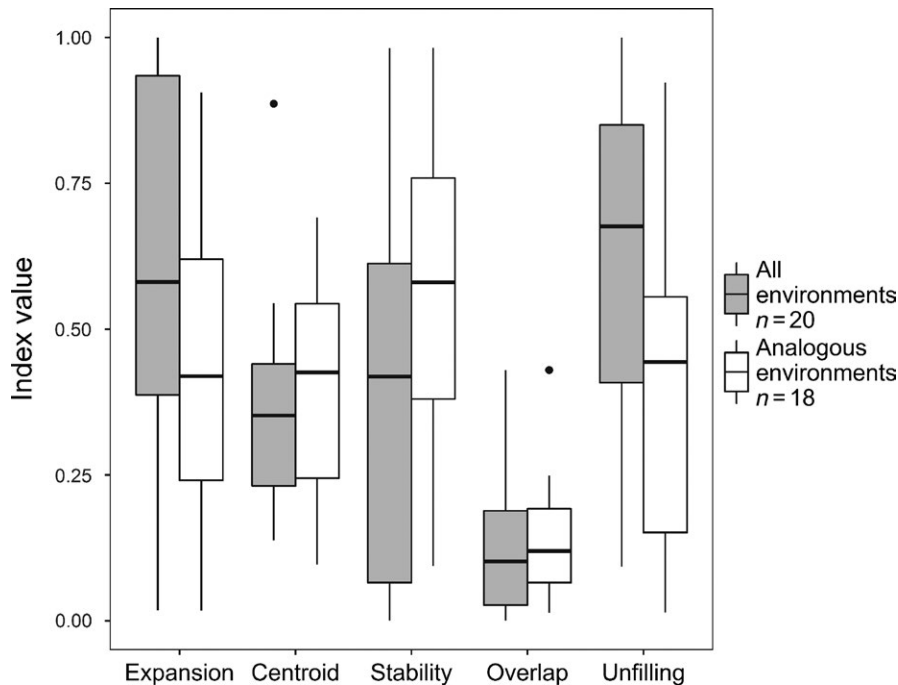
FIGURE 2 Boxplot of the niche metrics computed in all environments (*n* = 20) and only analogous environments (*n* = 18). The bar represents the median value and the upper and lower hinges the 25th and 75th percentiles, respectively. For two species, the metrics in analogous environments were not able to be computed because their entire native and invasive niches were in nonanalogous environments

were overlaid. These areas were defined by projecting New Zealand locations, with their associated climatic characteristics, within the two principal component axes used for the niche analysis of each species. With this procedure, New Zealand locations that intersected with niche stability climates of each species were identified, and subsequently, these areas were overlaid to obtain hotspots of niche stability. Three species were not included in this analysis because for two species (*D. villosus* and *H. anomala*), there were insufficient records in the native range and because the third species (*Potamopyrgus antipodarum*) is native to New Zealand.

To facilitate conservation or biosecurity planning, we also described hotspots of potential invasion using freshwater biogeographic units. These biogeographic units were delimited by Leathwick, Collier, and Chadderton (2007) and they correspond to geographic units having similar physical disturbance regimes, colonization pathways, natural barriers and native communities of vertebrates and invertebrates. To prioritize hotspots of invasion, we combined niche stability and climate suitability information. For each species, each pixel within a biogeographic unit was given a high risk of establishment if the pixel was climatically suitable for the species (predicted $p > 0.5$) and if the climatic characteristics of that pixel corresponded to the niche stability category. All analyses in this study were carried out using R (R Core Team, 2015), and the list of packages used can be found in Supporting information Appendix S10.

3 | RESULTS

3.1 | Niche conservatism in invasive freshwater invertebrates

For comparative purposes with other studies, a niche change of more than 10% was considered to be biologically significant (Parravicini

et al., 2015; Petitpierre et al., 2012). When niche changes were measured within all environments (i.e., analogous and nonanalogous environments), 90% of the species showed more than 10% of niche expansion and all species showed more than 10% centroid change (Figure 2, Supporting information Appendix S11 for individual results). Niche unfilling was also prevalent, and 95% of the species had at least 10% of their native niche that remained to be filled in the invaded range. However, some degree of similarity was observed between invasive and native niches where most of the species showed at least 40% of niche stability but interestingly, relatively low niche overlap. Stability measures the environments (cells) that are occupied in both invaded and native ranges, whereas the overlap metric measures the difference in occupancy between the ranges which is expected to be large, thus giving a low niche overlap. When considering niche changes only in analogous climates, the overall trends remained the same, where more than 80% of species indicated a change of at least 10% of centroid, niche expansion and unfilling (Figure 2, Supporting information Appendix S12). However, species showed slightly more niche stability when the metrics were computed in analogous environments.

Niches in the native and invaded ranges differed significantly for all species (niche equivalency test, Table 4). However for most species, environments from the invasion were consistent with environmental patterns seen in the native range (niche similarity test, Table 4) with the exception of *Eriocheir sinensis* (Milne-Edwards 1854, Varunidae), where the niche similarity test was rejected. Removing marginal climates using different thresholds had a significant effect on the quantification of niche expansion and unfilling (Friedman's rank-sum test, p-value < 0.00001), which suggests that for some species, part of their niche is found in marginal climates.

TABLE 4 Niche equivalency and similarity test results using niche overlap

Species name	Niche overlap	Niche equivalency	Niche similarity
Aedes albopictus	0.43	*	ns
Bithynia tentaculata	0.03	*	ns
Bythotrephes longimanus	0.02	*	ns
Cercopagis pengoi	0.03	*	ns
Cipangopaludina japonica	0.09	*	ns
Corbicula fluminea	0.19	*	ns
Dreissena polymorpha	0.08	*	ns
Dreissena bugensis	0.01	*	ns
Eriocheir sinensis	0.19	*	*
Gammarus tigrinus	0.00	*	ns
Limnoperna fortunei	0.09	*	ns
Orconectes limosus	0.13	*	ns
Orconectes virilis	0.14	*	ns
Pacifastacus leniusculus	0.11	*	ns
Pomacea canaliculata	0.25	*	ns
Potamopyrgus antipodarum	0.20	*	ns
Procambarus clarkii	0.21	*	ns
Pseudodiaptomus inopinus	0.00	*	ns
Rhithropanopeus harrisii	0.18	*	ns
Valvata piscinalis	0.06	*	ns

Notes. Niche overlap measures the intersection of two niches in the n-dimensional environmental space. Symbols and abbreviations: *(significant at p-value < 0.05) and ns (nonsignificant).

3.2 | Hotspots of invasion and niche stability in New Zealand

More than half of New Zealand was found to be climatically suitable for four to 11 species (Figure 3). In comparison, more than 25% of New Zealand corresponded to areas of climatic niche stability for four to 11 species (Figure 3). Interestingly, some hotspots of niche stability overlapped with hotspots of invasion, for example some areas of the northern Northland (Figure 4). However, in some areas, such as Auckland, hotspots of invasion were not identified as hotspots of niche stability.

Closer examination of specific biogeographic units showed at least nine of 29 units had more than half their area at risk for at least two species (Figure 5). The biogeographic units that should be carefully monitored are Auckland, Banks Peninsula, Canterbury, Clutha, northern and western Northland, Otago Peninsula, Taieri and Waitaki. In the context of prioritizing surveillance resources, however, Northland could be considered at higher risk than Auckland, because many species are likely to thrive due to the combination of climate suitability and niche stability conditions in those areas (Figure 4).

4 | DISCUSSION

This study provided for the first time an extensive assessment of the frequency of niche shift in invasive freshwater invertebrates.

Moreover, using New Zealand as a case study, this research proposed a novel framework to prioritize areas of high risk of invasion by combining information on niche conservatism and climate suitability. Thus, when resources are limited, surveillance can be targeted to areas where species are more likely to thrive and cause impacts.

4.1 | Niche conservatism

Although we might expect to observe niche conservatism, the niche equivalency tests we performed demonstrated significant niche shifts (Table 4). Most of the species (90%) showed changes in their niche measured by their centroid and expansion metrics (Figure 2). Even when considering the most conservative results after removing nonanalogous climates, more than 80% of the aquatic invertebrates did not retain their native climatic niche within the invaded range. These results suggest that niche shifts are more common for freshwater invertebrates than they are for other organisms, even in comparison with groups showing high frequency of niche shifts (57% for herpetofauna and 54% for insects; Li et al., 2014; Hill et al., 2017). For marine fish, birds and plants, only 33%, 29% and 14% of the species showed niche shifts, respectively (Parravicini et al., 2015; Petitpierre et al., 2012; Strubbe et al., 2013). The fact that aquatic species appear to show less niche conservatism than other organisms could be due to several reasons. Some niche shifts could be the result of not including other variables important for defining the species niche. For instance, using birds as case study, Strubbe and Matthysen (2014) found that
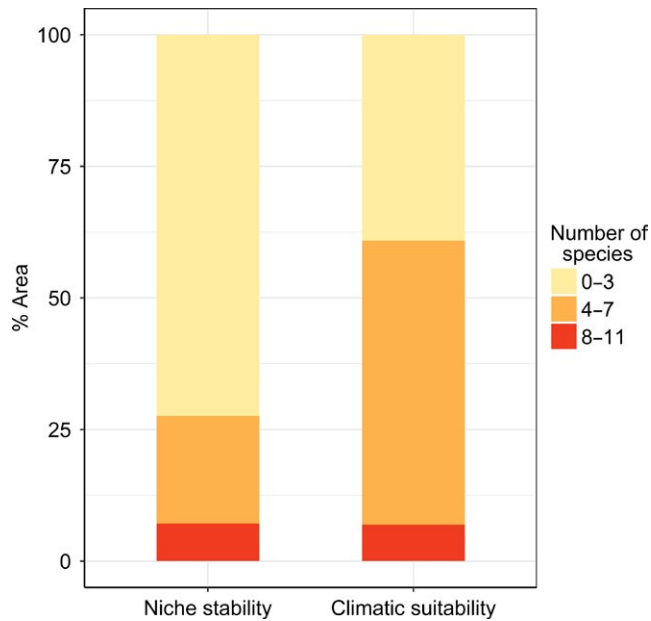
FIGURE 3 The bar diagram indicates the percentage of total area in New Zealand that is climatically suitable and matches niche stability environments for multiple invasive freshwater invertebrates (19 species) [Colour figure can be viewed at wileyonlinelibrary.com]

niche shifts were less common along precipitation seasonality, which is an important variable in both native and invaded ranges, in comparison with other variables that have a localized impact on only one range. Other nonclimatic factors such as freshwater variables and anthropogenic influence clearly need to be investigated to determine their effect on the quantification of niche shifts (Gallardo, Zieritz, & Aldridge, 2015; González-Moreno, Diez, & Richardson, 2014) but separately from macroclimate factors, to assess their relative effect (Guisan et al., 2014). Unfortunately, variables directly relevant to freshwater species, such as water chemistry or flood regimes, are not readily available at global scale (Loo, Keller, & Leung, 2007).

The high prevalence of niche unfilling in freshwater organisms might be due to the inability of these organisms to colonize all suitable habitats. Many of the species studied are recent introductions (Liebig, Benson, Larson, & Makled, 2016; Litsinger, Joshi, & Cowie, 2013; Mills, Leach, Carlton, & Secor, 1993), and dispersal can be modest for some of these species. Indeed, Strubbe et al. (2013) estimated that birds having recent introduction history showed more niche unfilling which reflects the ongoing dispersal in the invaded range. Additionally, for freshwater invertebrates, their particular dispersal strategies may slow down dispersal in their invasive range, potentially resulting in more niche unfilling. With the exception of flying insects, most freshwater species have passive dispersal that depends on wind, drift and other animals, for which they have to possess specific traits, such as resting stages and specific body adaptations for hitchhiking (Bilton, Freeland, & Okamura, 2001; Havel, Kovalenko, Thomaz, Amalfitano, & Kats, 2015). Therefore, it is mainly human-assisted dispersal that will promote their spread at a large scale, especially for those species lacking the aforementioned characteristics.
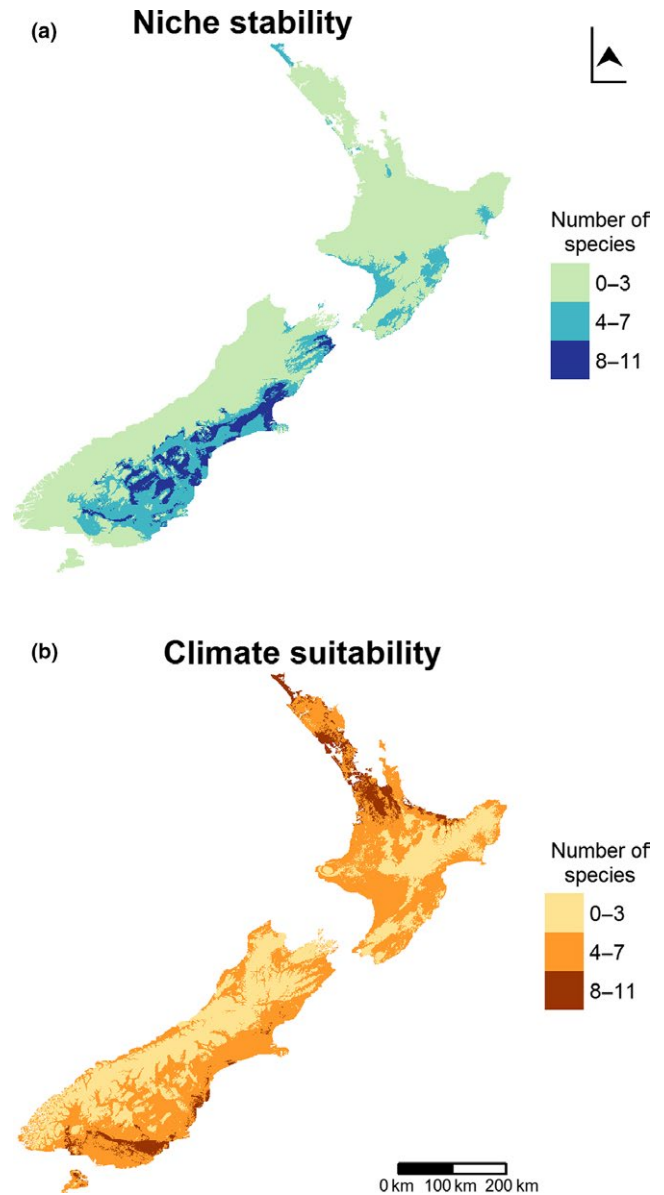
FIGURE 4 (a) Map representing potential hotspots of niche stability and (b) potential hotspots of invasion assessed by climatic suitability. See Figure 5 for locating the biogeographic units [Colour figure can be viewed at wileyonlinelibrary.com]

In this research, species showed significant realized niche expansion in both analogous and nonanalogous environments. We also found that some of the niche changes were observed in marginal climates in the native and/or invaded range. There is an ongoing debate about the mechanism for niche change in analogous and nonanalogous environments (Guisan et al., 2012; Webber et al., 2012). Indeed, differentiating evolutionary mechanisms from other ecological mechanisms for niche expansion in nonanalogous environments is challenging considering that the species did not have those environments available in its native range. What is clear is that changes in the fundamental niche cannot be detected with distribution data. Colonization of new environments in the invaded range not occupied in the native range could be the result of the absence of biotic interactions such as enemy release or absence of competition
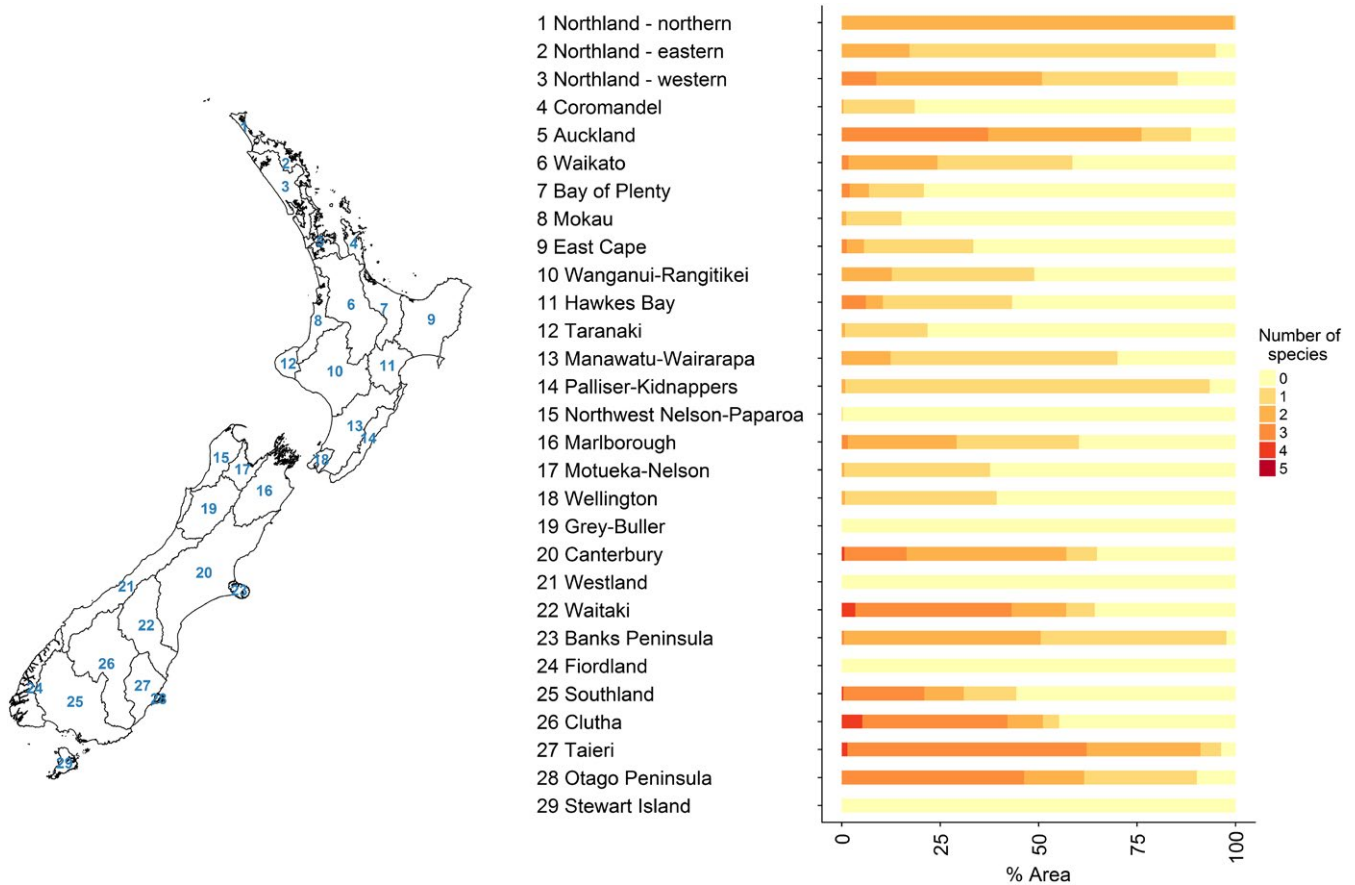
FIGURE 5 Map represents biogeographic units in New Zealand suggested by Leathwick et al. (2007). The bar diagram illustrates the percentage of area by biogeographic unit that is at high risk of invasion by multiple species. High risk of invasion is indicated when locations are climatically suitable and their environments matched niche stability environments [Colour figure can be viewed at wileyonlinelibrary.com]

(Catford, Jansson, & Nilsson, 2009). For example, one of the species investigated, *Orconectes virilis* (Hagen, 1870, Cambaridae), can be infected in its native range by a parasite, *Microphallus* spp., making it more vulnerable to predation than in its invaded range where the parasite has not been reported yet (Reisinger, Petersen, Hing, Davila, & Lodge, 2015). Furthermore, Hill and Lodge (1999) reported that *O. virilis* is outcompeted in its native range by another invasive species, *O. rusticus*. Similarly, *Potamopyrgus antipodarum* (Gray 1843, Hydrobiidae) native populations can show a high incidence of parasitic trematodes, whereas in the invasive range their incidence is very low (Alonso & Castro-Díez, 2012). Such examples illustrate that biotic exclusion in the native range could lead to a realized niche expansion in the invaded range. The realized niche may also change when natural dispersal barriers are transgressed. For example, island endemics such as *P. antipodarum* can occupy new environments in the invaded range because of preadaptation to those environments (Alexander & Edwards, 2010). However, challenges remain to differentiate between an evolutionary change, phenotypic plasticity and ecological responses (Moran & Alexander, 2014). For instance, *Corbicula fluminea* (Müller 1774, Cyrenidae) and *Dreissena bugensis* (Andrusov 1897, Dreissenidae) both show morphological plasticity in their invaded range; however, whether this response resulted in

increased fitness as required to persist in the new area has not been demonstrated yet (Peyer, Hermanson, & Lee, 2010; Sousa et al., 2007). Asian tiger mosquito (*Aedes albopictus*) has been shown by Lounibos et al. (2003) to provide a good example of spread assisted by rapid evolution where its photoperiodically induced diapause has changed in the northern latitudes of the USA in response to early arrival of winter days and reduced in more southern latitudes to exploit longer days. Likewise, multiple invasions of the copepod *Eurytemora affinis* (Poppe 1880, Temoridae) in North America and Asia were followed by an osmoregulatory evolution that allowed the species to shift from native saline habitats to freshwater habitats (Lee, 2015).

The SDMs used in the study were able to correctly predict the majority of the presences in the invaded range (~70%) for most species, with the exception of *Bithynia tentaculata*, *Orconectes virilis* and *Valvata piscinalis* (Supporting information Appendix S8). For these species, there were fewer presences available in the invaded range which might explain the poor performance of the models to predict their invaded distribution (Supporting information Appendix S1). These results highlight the importance of having adequate data for the invaded range distribution, particularly when there is evidence of niche shift. To account for niche shift when implementing correlative SDMs, Broennimann and Guisan (2008) recommended using

both native and invaded distributions. However, when the invasive range is poorly known, correlative SDM may not able to characterize adequately invaded distributions. Other models such as mechanistic SDMs may help address this issue by including some ecological processes omitted by correlative SDMs (Dormann et al., 2012). However, such models require extensive knowledge derived from complex experimentation or observation. Such data are often unavailable, particularly for poorly known invasive species.

4.2 | Implications for risk assessment, surveillance and management

In this study, we identified a number of species showing significant niche changes (Supporting information Appendices S11 and S12). Detecting niche changes in the realized niche may reveal concealed ecological or evolutionary processes that allow species to colonize new environments. Thus, considering niche changes enables species that might challenge surveillance and management processes to be identified. The information on niche changes could also be used in an invasive species risk assessment. Typically in risk assessments, several criteria are considered such as the presence of host, environmental characteristics of the area of interest and biological factors that make the species to be of particular concern (Pearson, 2006). Species experiencing high niche expansion could be of higher concern as they have demonstrated the ability to colonize new environments.

Further examination of where these changes occur may then help to determine potential control strategies. For example, analogous environments that are colonized in the introduced range but are not in the native range could indicate the presence of an "enemy" in the native range that could be used for biological control. Only experiments using the populations that showed niche changes will reveal the true mechanism behind this change. For instance, a comprehensive framework such as that used by Rey et al. (2012) and Krehenwinkel et al. (2015) could shed light on the evolutionary mechanisms behind climatic niche shifts. Their framework combine species distribution modelling, experimental and genetic approaches. By initially detecting climatic niche shifts and then sampling populations exhibiting changes of the tropical ant *Wasmannia auropunctata*, Rey et al. (2012) were able to show experimentally that adaptation to cold occurred in the native range, before the species invaded the Mediterranean area.

Ours is the first study to combine hotspots of invasion and niche conservatism. This combination is a useful way of prioritizing areas for monitoring and surveillance. For instance, despite not being identified as a hotspot of niche conservatism, the Auckland area in the upper region of New Zealand's North Island was identified as high risk because it was shown to be climatically suitable for at least eight invasive freshwater species (Figure 4). However, within the context of prioritization of areas for surveillance and monitoring, the Auckland area could be considered less critical compared with Northland (further north) where hotspots of invasion match hotspots of niche stability and thus where the species are more likely to establish based on climatic requirements.

5 | CONCLUSIONS

This research shows that niche conservatism in invasive freshwater invertebrates is the exception rather than the rule, highlighting the challenges for anticipating their impact on freshwater ecosystems. We showed that New Zealand is generally climatically suitable for many invasive freshwater invertebrates and identified biogeographic units that are at most risk, using a novel approach to prioritize those areas. In New Zealand, unintentional introductions of high-risk species, particularly microinvertebrates or species having dormant stages such as diapausing eggs, could likely occur through the aquarium trade (Collier et al., 2011; Duggan, 2010) or on recreational equipment, such as fishing and sports gear (Smith & Dodgshun, 2008). Such pathways should be carefully considered along with the identification of suitable areas for establishment and potential hotspots, as highlighted in this study, for more effective prioritization of areas for surveillance and monitoring.

ORCID

Ursula Torres http://orcid.org/0000-0002-7640-0823

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BIOSKETCH

Ursula Torres is a quantitative ecologist with an interest in the development and use of spatial models for supporting the management of invasive species, conservation of biodiversity and food security. She is particularly passionate about macroinvertebrates and birds. She is currently working as a risk analyst in biosecurity for the Ministry for Primary Industries of New Zealand.

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SUPPORTING INFORMATION

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